ISSN 0582-415X

西水研研報
Bull. Seikai Natl. Fish. Res. Inst.
(78), 2000

BULLETIN
OF
SEIKAI NATIONAL FISHERIES RESEARCH INSTITUTE

No. 78
June 2000

西海区水産研究所研究報告

第78号

西海区水産研究所
長崎市国分町3番30号

平成12年6月

Analysis of Water Mass Distribution in the East China Sea Using Sea Surface Temperature Data

Kenji Morinaga, Osamu Katoh, Norihisa Nakagawa and Makoto Fujita

Bull. Seikai Natl. Fish. Res. Inst., (78), 1－12 (2000)

Focussing on the variability of water mass distribution in the East China Sea, we considered temporal and spatial variations of sea surface temperature (SST). As a result, it was found out that the Kuroshio branch expanded further north in winter and the Kuroshio water spread on the continental shelf in summer. From the variance and the average year position of the Kuroshio water west of the Kyushu Island, it was found out that the position of the Kuroshio water was so stable in winter. However, it is suggested that the year-to-year variations were remarkably large in summer. The average year position of the Kuroshio water has been shifted westward gradually since 1987, and the autocorrelation function calculated by the running mean value shows 2.25-years periodicity.

Key words: sea surface temperature, the East China Sea, water mass distributions, annual changes

Behavioral Response of Sharks to Electric Stimulation

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Bull. Seikai Natl. Fish. Res. Inst., (78), 13－30 (2000)

The behavioral responses of sharks to electric stimulation were studied. We used two methods of electric stimulation, one is the Electric Field Experiment (EFE) and the other is the Partial Electric Field Experiment (PEF). In the EFE, all sharks swam close to the side of the tank when the signal generator was off. When the 60 Hz sine wave and DC pulse electric field were being produced, two species, *Carcharhinus falciformis* and *Triaenodon obesus*, immediately turned around. The sharks were demonstrated a high rate of turning when exposed to the DC pulse electric fields. Conversely, *Stegostoma fasciatum* did not change its swimming patterns when the signal generator was on. In the PEF, four species, *Carcharhinus melanopterus*, *C. falciformis*, *T. obesus*, and *Triakis scyllium*, gave a strong response to the electric field, two species, *Caphaloscyllium isabellum* and *Scyliorhinus torazame*, gave a weak response to the electric field, but two other species, *G. cuvier* and *S. fasciatum*, did not show a response to the electric field. Hence, the behavioral response patterns were different among the species.

Key words: sharks, ampullae of Lorenzini, electric stimulation, behavioral response, swimming pattern

Species Composition of Epifauna and Infauna on Intertidal Boulder Shores at Ishigaki Island in Subtropical Japan

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Bull. Seikai Natl. Fish. Res. Inst., (78), 31−47 (2000)

Species compositions of intertidal epifauna and infauna were quantitatively investigated on boulder shores at Ishigaki Island in subtropical Japan. These faunae were collected by quadrat for 4∼5 seasons×3 shores×5∼6 heights. In total, 112 species in epifauna and 27 species in infauna were collected. Among epifauna, species number was higher in mobile animals (97 species) than in sessile ones (15 species). Among the mobile animals, species number was highest in Gastropoda (68 species), in which *Nerita squamulata* was abundant (the highest density for each shore: 50.0 to 500.0 m^{-2}). Among the sessile animals, however, species number was highest in Bivalvia (14 species). Among infauna, species number was highest in Bivalvia (26 species) which abundantly included *Asaphis violascens* (the highest density for each shore: 12.0 to 83.0 m^{-2}) and *Ruditapes variegatus* (5.6 to 26.0 m^{-2}), holding edible molluscs as many as 10 species. The species composition of these faunae varied 1) among shores, more sharply for epifauna than for infauna; 2) among seasons, sharply for both faunae on some shores; and 3) among heights, sharply for both faunae. Such variations in species composition and the rareness of sessile species are discussed in relation to unique environments of boulder shores.

Key words: intertidal epifauna and infauna, species composition, boulder shores, subtropical island

Relationship between Cd and PO_4 off the Ryukyu Islands.

Kazuo Abe

Bull. Seikai Natl. Fish. Res. Inst., (78), 49−56 (2000)

Relationship between Cd and PO_4 off the Ryukyu Islands was investigated in May 1998. Preformed Cd and PO_4 were nearly zero in surface layer and increased with depth below 400 m, and reached approximately 0.7 nM and 1.2 μM, respectively in deep water (below 1,000 m). The relationship between Cd and PO_4 showed a clear deviation. Above 400 m, the slope of the regression line was 0.131 ($nM_{Cd}/\mu M_{phosphate}$), and this value was much the same as the regeneration ratio of Cd to PO_4, which suggested that regeneration process might be a main factor that regulated the correlation of Cd and PO_4 in this layer. Below 400 m, the Cd/PO_4 ratios increased gradually with depth to the almost constant value of 0.36 (nM/μM) below 1,000 m, which is considered to be attributable to the apparent conservative mixing between water masses with originally different Cd/PO_4 ratio (different preformed values), in deep and shallow layer.

Key words: Dissolved Cd, phosphate, the Ryukyu Islands, AOU

Recovery of *Ecklonia kurome* after the Occurrence of Blade Disappearing Phenomenon at Nomozaki, Nagasaki Prefecture
Setuo Kiyomoto, Taku Yoshimura, Shogo Arai, Takaya Kiriyama, Akihiko Fujii and Toshio Yotsui
Bull. Seikai Natl. Fish. Res. Inst., (78), 57−65 (2000)

In autumn of 1998, the blade disappearring phenomenon assumed to be results of grazing by herbivorous fishes was observed on *Ecklonia kurome* along the shallow coastal waters at Nomozaki. We investigated the recovery of *E. kurome* after the autumn event at Ôtategami–iwa and Kotategami–iwa in Nomozaki area until the following spring. At Ôtategami–iwa, the thalli having regenerated blades were observed in shallower than 2 m depth, but did not in deeper than 3 m depth. At Kotate-gami–iwa, 2 km distant from the Ôtategami–iwa, the thalli having regenerated blades were recognized in all the depth from 0 to 13 m, and dense *E. kurome* beds as well. From the existence of arc–shape scars on the newly growing blades collected at the two sites on March 1999, the grazing by herbivorous fishes was thought to have continued during the following winter. The differences in degree of recovery between the two sites and among different water depths may be resulted from the continuity and intensity of the grazing by fishes. During these investigations, we also found remarkable undergrowth of *Sargassum hemiphyllum* and *Hizikia fusiformis* having no apical growth point in the shallow waters. These phenomena were presumed to be caused by the grazing of herbivorous fishes, different from those consumed *E. kurome*.

Key words: *Ecklonia kurome, Sargassum, Hizikia,* disappearing blade, grazing, herbivorous fish.

Grazing Selectivity of Herbivorous Fishes on Five Macroalgae in Sublittoral Zone at Nomozaki, Nagasaki Prefecture

Setuo Kiyomoto, Taku Yoshimura and Shogo Arai

Bull. Seikai Natl. Fish. Res. Inst., (78), 65–75 (2000)

Based on an assumption that grazing by herbivorous fishes is one of important factors responsible for the large scale disappearance of macroalgae blades, grazing selectivity of these fishes on large brown algae was studied in sublittoral zone at Nomozaki in Nagasaki Prefecture, Japan. Five species of brown algae, *Undaria pinnatifida, Ecklonia kurome, Sargassum macrocarpum, S. yendoi*, and *S. serratifolium*, were sampled on March in 1999 and arc-shape scars on each individual were investigated in detail.

The proportion of individuals having blades less than half of the normal blade area was 83% in *U. pinnatifida*, clearly higher than that of 0 to 3 % in the other 4 species. Also, the proportion of individuals having arc-shape scars, thought to be the evidence of grazing, was 93% in *U. pinnatifida*, 23% in *E. kurome*, and less than 5 % in the remaining 3 species. These results clearly indicate selective grazing by herbivorous fishes on *U. pinnatifida*.

The scars on the midrib of *U. pinnatifida* closely resembled the tooth marks artificially made by pressing the teeth of *Calatonus japonicus*, therefor *C. japonicus* is thought to be one of the grazers. More researches are needed to make clear participation of another fishes in grazing activity, and to elucidate the influences of fish grazing on the community structure of algae.

Key words : Brown macroalgae, *Undaria pinnatifida, Ecklonia kurome, Sargassum, Calatonus japonicus*, herbivorous fish, grazing

表面水温から見た東シナ海の水塊分布

森永　健司*・加藤　修**・中川　倫寿*・藤田　真***

Analysis of Water Mass Distribution in the East China Sea Using Sea Surface Temperature Data

Kenji Morinaga*, Osamu Katoh**, Norihisa Nakagawa* and Makoto Fujita***

ABSTRACT

Focussing on the variability of water mass distribution in the East China Sea, we considered temporal and spatial variations of SST, and described schematical representations of water mass distributions in both winter and summer in the East China Sea. From those results, in winter, it was found out that the Kuroshio water called the Kuroshio branch reached to 28° N, 124° E northeast of the Taiwan, the Yellow Sea cold water expanded to 27° N east of the Kuroshio branch (north of the Miyako Island), and the northern limit of the Kuroshio water was at 32° N and overlay westward to the Danjyo Islands (32° N, 128° E). And in summer, it was found that the distribution area of the Kuroshio branch became smaller than in winter and the Kuroshio water spread on the continental shelf than in winter off the westcoast of the Kyushu Island.

Additionally, from the variance and the average year position of the Kuroshio water west of the Kyushu Island, it was found out that the position of the Kuroshio water was so stable in winter. However, it is suggested that the year-to-year variations were remarkably large in summer from the variance of the average year position. The average year position of the Kuroshio water has been shifted westward gradually since 1987, as its annual changes were analyzed from

平成11年12月27日受理（Recieved December 27, 1999）
西海区水産研究所業績第596号（Contribution from Seikai National Fisheries Research Institute, No. 596）
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the 13-months running mean value. Moreover, the autocorrelation function calculated by the running mean value shows a strong peak of 27-month lag time, that is, periodicity in 2.25 years could be recognized.

は じ め に

広い大陸棚を有する東シナ海は，世界でも有数の好漁場であり浮魚・底魚を問わず多種多様の漁獲がある．これは長江・黄河から東シナ海へ流出する淡水が栄養塩を大量に補給するために，一次生産が活発となり魚類の餌環境がきわめて良好であることに起因するものと考えられている．これまで水産海洋学的視点からは，東シナ海の海況変動に大きな影響を及ぼす黒潮の変動や，日本海へ流れ込む対馬暖流の形成過程が研究対象となってきた．

東シナ海の海況について，小泉（1964）は10年間の西日本海況旬報（長崎海洋気象台）をもとに表面水温の平年値からの標準偏差分布を求め，その分布特性から東シナ海を黒潮型，黄海冷水型変動の2つの領域に分類した．Moriyasu（1967）は同様の資料を用いて自己・相互相関関数を求め，表面水温が水塊の類型化に有効であることを示した．また土田（1975）は，20年間の西日本海況旬報をもとに表面水温の月毎の統計値を求め，夏・冬期における表面水温分布の特徴について考察した．その結果，済州島南方（32° N，126° E）と長江東方（30° N，125° E）に特徴的な水域があることを報告している．近藤（1985）は，東シナ海北部に黄海冷水，長江河口を中心とする東シナ海西部に大陸沿岸水，東シナ海南部に黒潮系暖水が分布し，それぞれから派生した水塊が混合・変質した後に東シナ海東部で対馬暖流の源流を形成するとして，東シナ海の水塊分布概念図を作成した．他方，表面水温変動の周期性に注目した金子ら（1987）は，30年間の西日本海況旬報をもとに作成した月毎の表面水温資料をもとにFFT による周期解析を行った．その結果，大陸棚上の表面水温には2年および6年の卓越変動周期が顕著に認められること，さらに2年周期の変動成分を抽出して空間的なコヒーレンスを求めた結果，済州島南方に特異的な海域が存在することを報告した．

漁海況予報に関して最も重要となるのは経年的および季節的な変動傾向を把握することである．上記各水塊の物理特性および分布域は短期的かつ複雑に変化することを考慮すれば，平年値を用いての解析ではあっても基礎となる資料の観測間隔がより短く，ある程度長期的に得られる資料を解析に用いることが望まれる．そこで，本研究では週毎に得られる東シナ海海況速報（漁業情報サービスセンター）および CTD 観測資料を用いて，東シナ海での経年的・季節的な海況変動特性を考察する．

資 料 と 方 法

東シナ海海況速報（漁業情報サービスセンター）より，緯度・経度各1°毎の格子点における水温値を比例配分して読み取り，解析に用いる表面水温資料を作成した．作成した資料の期間は1986年4月～1996年3月の10年間である．また，資料の有意性を考慮して，上記期間に取得可能な総データ数の90%かつ各月で取得可能なデータ数の50%以上の資料が得られた格子点（60点）に限定して月毎に平年水温を算出し解析を行った．解析に使用した格子点は Fig. 1 に示すとおりである．また，各水塊を代表する測点としては，近藤（1985）の水塊分布図を参考に，黄海冷水に A 点，黒潮系暖水に B 点を選択した（Fig. 1）．また，夏期の水温変動の特徴を検討するために，以下の式で求められる指数 s を導入した．

$$s_i = (| T_i^7 - T_i^8 | + | T_i^8 - T_i^9 |) \times 10$$

T_i^j：水温平年値（i は格子点番号，j は月を示す）

加えて，東シナ海の水温鉛直分布の季節的な特徴を示すために，長崎海洋気象台が北緯32° N に沿う観測線で1992年に実施した CTD 観測資料を用いた（Fig. 2a～d).

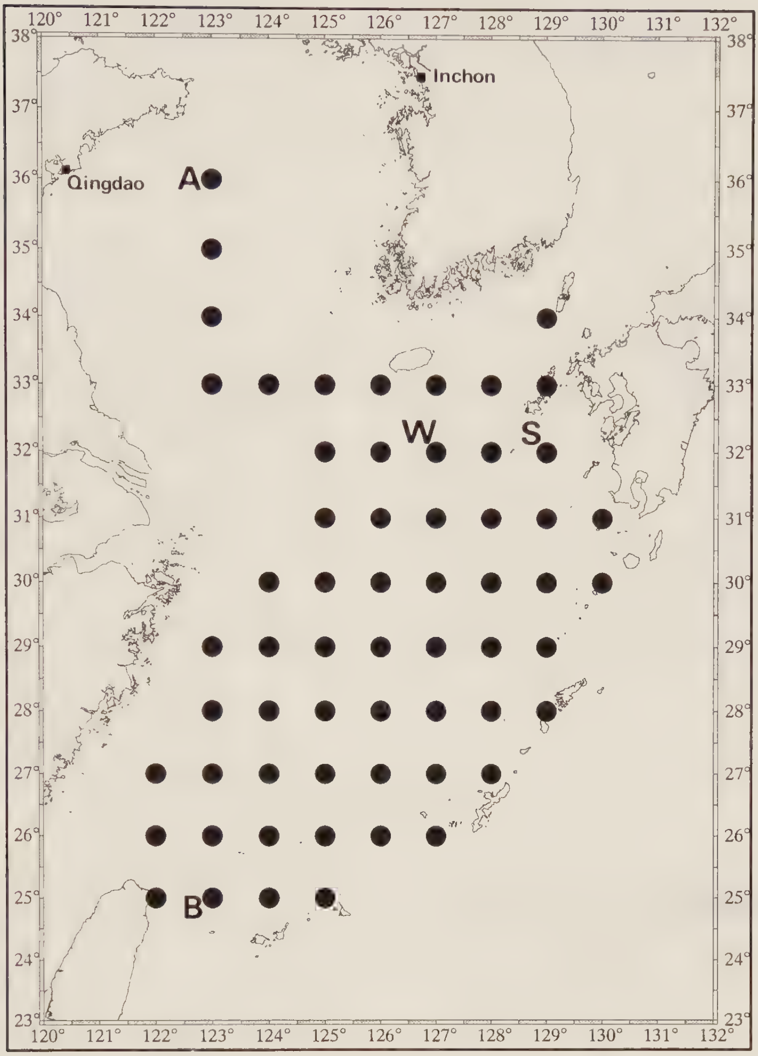


Fig. 1. Station locations used to analyze the characteristics of the temporal and spatial variations of sea surface temperature in the East China Sea. A and B shows the representative points as the Yellow Sea cold water and the Kuroshio water, respectively. W and S are the points which showed as a character water temperature in winter or summer, respectively.

1．冬期の表面水温変動による水塊の類型化と水塊分布の特徴

冬期，東シナ海では大気による冷却作用により強い鉛直混合が生じ，例えば Fig. 2a に示されるように，水温・塩分の等値線ともに海面から海底にまで達する状況を呈する．すなわち冬期においては底層の水塊分布が海面に反映されるものと考えられ，２次元的な水塊分布様式を考慮することができる．Fig. 2a～d より100m以浅での水温鉛直分布を見ると，10月および２月の観測結果では等温線，等塩分線ともに鉛直方向

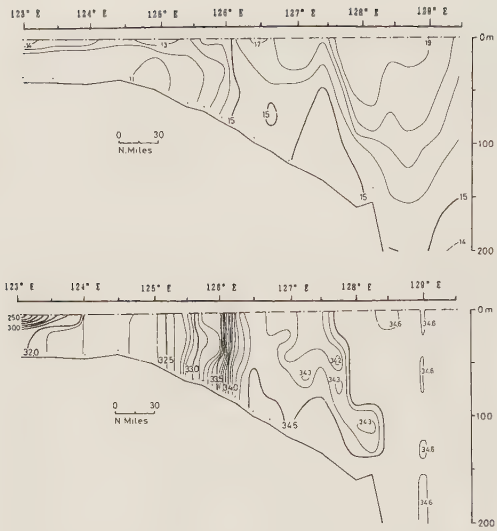


Fig. 2a. The oceanographic observation section along 32°N in February, 1992. The upper panel shows temperature, the lower salinity (after Nagasaki marine observatory, 1992a).

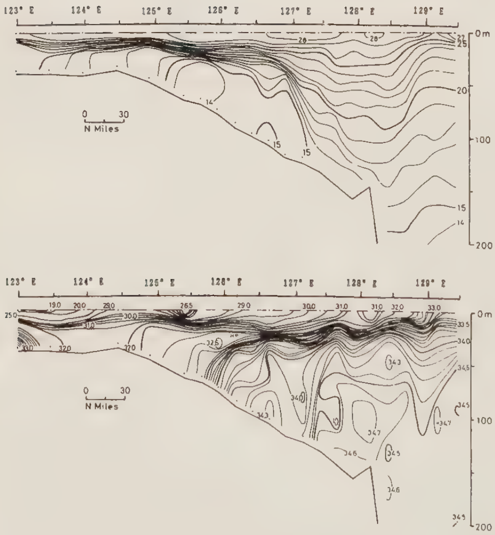


Fig. 2b. The same as Fig. 2a, except in April, 1992 (after Nagasaki marine observatory, 1992b).

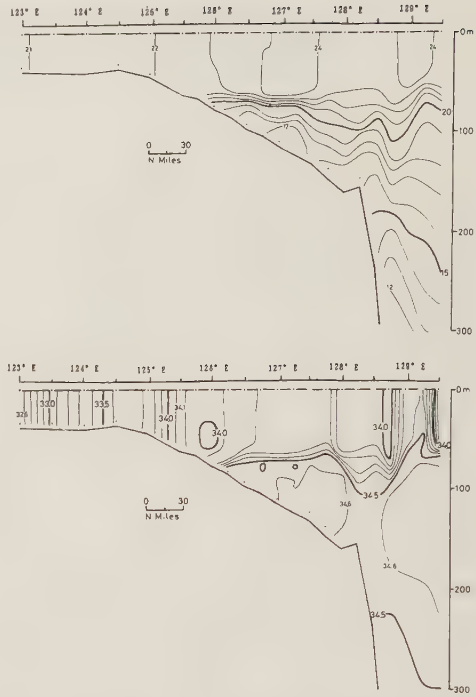


Fig. 2c. The same as Fig. 2a, except in July, 1992 (after Nagasaki marine observatory, 1992c).



Fig. 2d. The same as Fig. 2a, except in October, 1992 (after Nagasaki marine observatory, 1992d).

に描かれている．これは強い鉛直混合が生じたことによるものと考えられる．4月の観測結果では等温線，等塩分線が水平的に描かれており，鉛直混合が若干弱まるものと推察される．一方，黄海冷水を代表するものと考えられるA点（Fig. 1）での表面水温の平年値とA点をはさむ青島と仁川での気温の平均値から求めた平年値を比較すると，Fig. 3 に示すように8月～3月まで水温が気温に比べて高い傾向にあり，大気による冷却効果は3月まで持続するものと推察される．そこで本節では海面冷却により鉛直混合が盛んとなる期間（10月～3月）を冬期と定義する．

皆川（1997）は，大陸沿岸水の主要な起源水と考えられる長江からの淡水流量（漢口（Hankow）での水位より求められた流量の平年値）は1月に年間最低値を示すこと，さらに冬期5カ月間での積算流量（169.4 $\times 10^9 m^3/sec$）は最大流量を示す8月の流量（119.2 $\times 10^9 m^3/sec$）の150％にも満たないことを報告している．以上の結果より，冬期には大陸沿岸水の分布域は狭い範囲に限られるものと推測されるため，冬期の東シナ海における水塊分布特性の把握に際して，主に黄海冷水と黒潮系暖水に限定して考察を進めるものとする．

黄海冷水と黒潮系暖水の表面水温変動を最もよく表わしていると考えられる格子点A，Bでの月毎平年値を Fig. 4 に示す．土田（1975）に示されているとおり，年平均水温はAでは低くBでは高いこと，季節変動巾はAでは大きくBでは小さいことが分かる．また，B点では2月に年間最低水温を示すのに対してA点では3月に最低水温となり，1カ月の遅れが認められる．そこで本報告では冬期における黄海冷水と黒潮系暖水の定義を，それぞれ3月，2月に年間最低水温を示す水塊とする．この変動特性を2つの水塊の識別基準として，東シナ海での冬期における平年的な水塊分布図を作成した（Fig. 5）．Fig. 5 をもとに黄海冷水および黒潮系暖水分布の特徴を以下に示す．

1）台湾北東方では，黒潮系暖水が28° N，124° E まで分布している．これは，台湾と与那国島間を通って東シナ海へ流入した黒潮系暖水の一部が，魚釣島付近

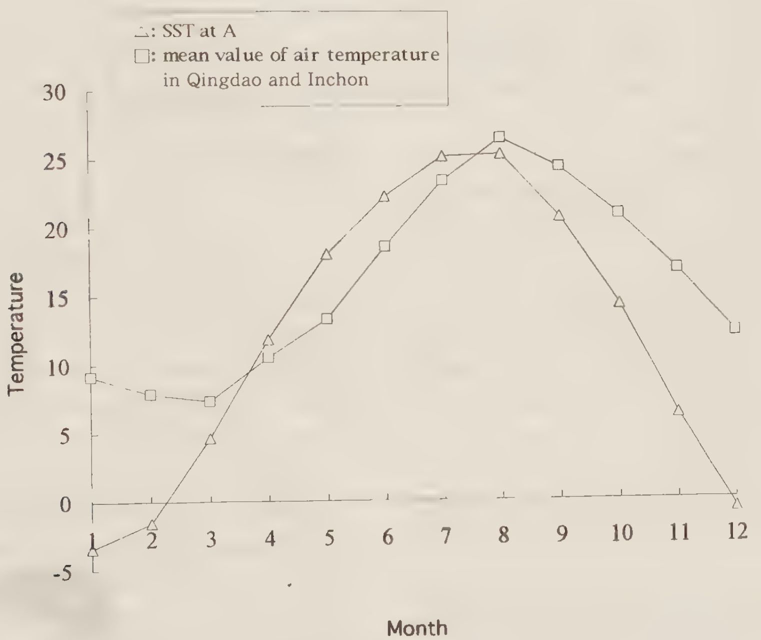


Fig. 3. Changes of an average year temperature, obtained from sea surface temperature in A (△: Yellow Sea cold water) and mean value of air temperature in Qingdao and Inchon (□).

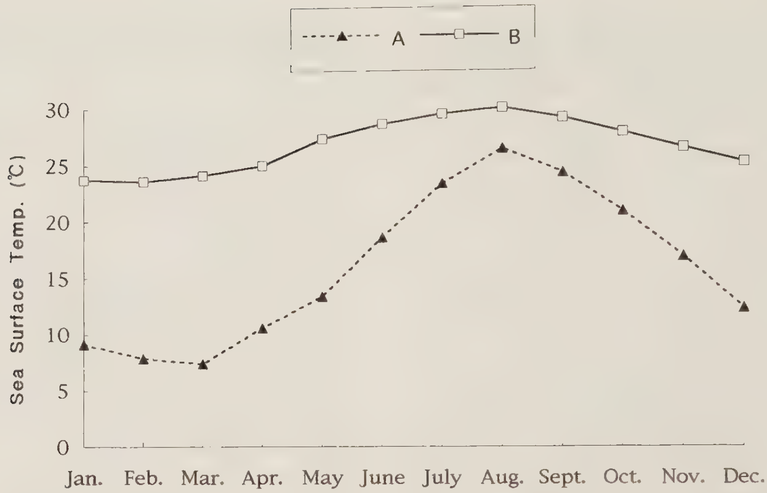


Fig. 4. Changes of an average year sea surface temperature in the representative points (A, B) as the Yellow Sea cold water and the Kuroshio water.

を東西方向にはしる大陸斜面を越えて大陸棚上の100m等深線付近にまで広がる状況を示している．いわゆる"黒潮分派"として知られる水塊を示すものである．

2）黒潮分派の東側（宮古島北方）では27° Nまで黄海冷水が分布している．これは黒潮分派の東側に南下流があり，この流れにより黄海冷水の分布域が南に張り出しているものと推測される．

3）126° E以東では黒潮系暖水が北東方向に分布している．この分布状況は，宮古島北方で大陸斜面の走向が北東方向に変化するために，黒潮の流路が北東方向へと変化することに起因するものである．

4）黒潮系暖水が認められる北源は32° Nであり，男女群島付近では分布域が32° N，128° Eへと西方に張り出している．この張り出した状況は，トカラ海峡西方で大きく変向する黒潮から北方へと分岐する暖水が男女群島付近まで分布していることを示唆するものである．すなわち，128° E付近を北上するものと考えられている対馬暖流の冬期における形成過程には，黒潮からの暖水の供給が重要であることを示唆している．

2．夏期における表面水温変動傾向からみた水塊分布の特徴

王・孙（1992）は，夏期において長江の流量と大陸沿岸水の分布面積との間に正の相関が認められることを報告している．夏期における水温・塩分鉛直断面（Fig. 2c, d）より，黄海冷水の上層に低塩分水が分布し，顕著な水温・塩分躍層が形成され強い成層が形成されていることが分かる．皆川（1997）によれば，6月には長江の流量が年間平均流量を上回ることから，本節では鉛直混合が始まる10月までの期間（6～9月までの4カ月間）を夏期として水塊分布特性を検討するものとする．

上述したように夏期の特徴は，長江流量の増加に伴う大陸沿岸水分布域の増加，および日射による表面水温の上昇により顕著な密度成層が表層に形成されることである．すなわち，冬期に形成された黄海冷水の上層に大陸沿岸水が分布することにより，表面水温への黄海冷水の影響は軽減されるものと考えられる．そこで本報告では，夏期の東シナ海における水塊分布特性の把握に当たり，大陸沿岸水と黒潮系暖水の分布域に関して検討する．

さて，Fig. 4 より夏期でも特に7～9月の水温変動は，黒潮系暖水が分布するB点では緩やかであるのに対して大陸系沿岸水が分布するA点では急激な変化を示す．A点の表面に分布する低塩分・低密度の水塊が日射により昇温し，一層密度が低くなって成層が強化され鉛直混合が阻害された結果，低密度化した水塊は表層付近に留まり日射によりさらに高温化すること

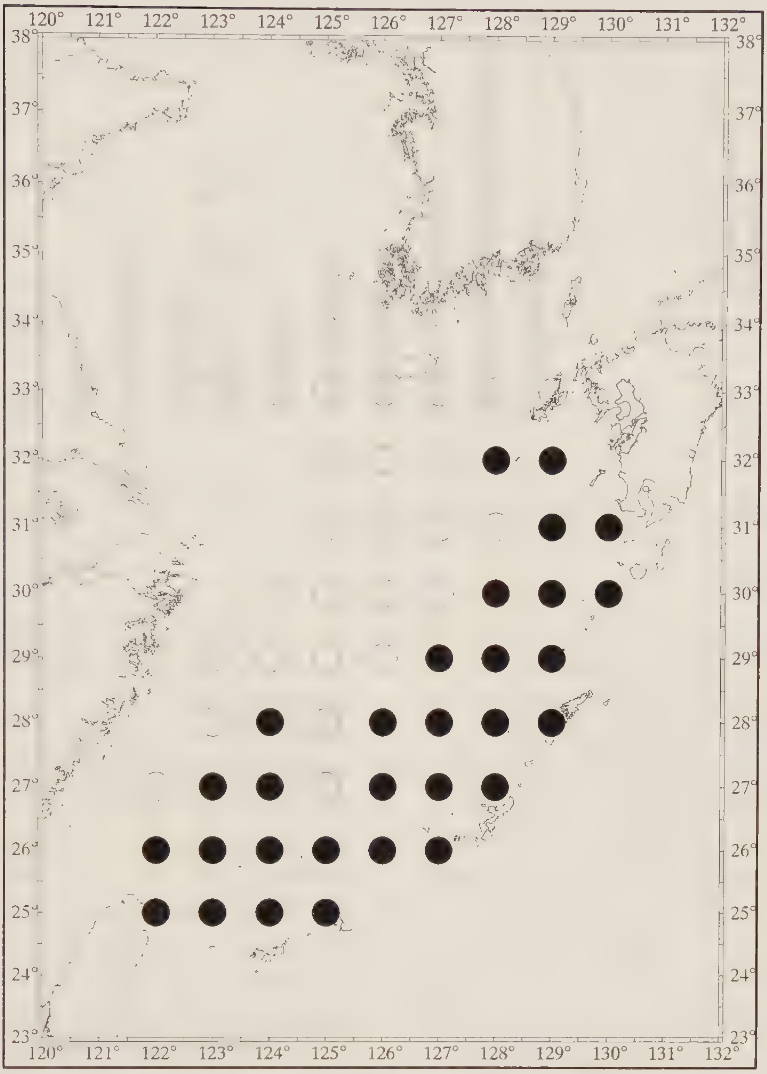


Fig. 5. An average year water mass distributions in winter in the East China Sea. White circles denote the Yellow Sea cold water grids, and solid circles denote the Kuroshio water grids.

が，上述の水温変動を引き起こす原因であると考えられる．夏期，大陸沿岸水は広域に分布し，前述の過程により昇温することから異水塊との水平混合による水温低下の効果が少ないことも高温化する一因であるものと推測される．

ここで7～9月にかけての特徴的な水温変化を指標として水塊分布を検討するために，前述の指数 s を導入する．指数 s は7，8，9月での水温変化量の和に相当し，緩やかに変化する B 点では小さく，反対に急激な変化を示す A 点では大きくなる．指数 s を各格子点で算出し，その頻度分布を Fig. 6 に示した．Fig. 6 より20～25，55～60を中心とする部分と，これらの中間の35～40を中心とする部分の 3 箇所に区分することができる．これらはそれぞれ黒潮系暖水，大陸系沿岸水およびこれらの混合水に相当するものと考えられる．以上の結果から黒潮系暖水を大陸系沿岸水および

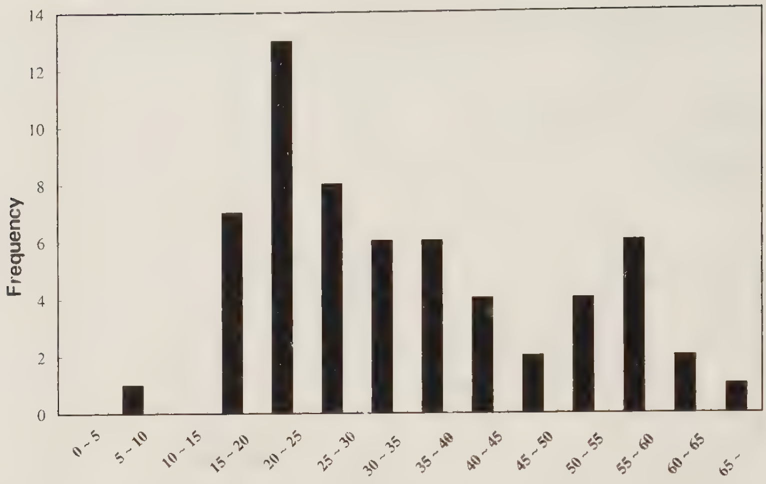


Fig. 6. Frequencies of classification index (s=$|T^7-T^8|+|T^8-T^9|$). calculated from averaged SST data.

混合水と区別するためにはs＝25で区分することが妥当である．そこで，s＜25の格子点には黒潮系暖水が，s≧25の格子点には大陸沿岸水が分布するものとして水塊分布図を作成した（Fig. 7)．Fig. 7 から，台湾北東方では黒潮系暖水の分布域が28° N，123°～125° Eにまで認められ冬期に比べて拡大していることが分かるが，潘ら（1990）は台湾海峡から北東方向に流れる台湾暖流が夏期に強勢となり黒潮分派の分布域が縮小するためであると推察しており，冬期に比べて拡大した海域には台湾暖流によって輸送された暖水が分布しているものと考えられる．宮古島北方から九州に至る海域での黒潮系暖水の分布域は，冬期に比べて陸棚斜面付近まで縮小している．また九州西岸沖では32° N，129° Eが黒潮系暖水の北限となり，ここでの分布域も冬期に比べて九州沿岸よりに分布し縮小していることが分かった．

以上の結果から，夏期の東シナ海の水塊分布の特徴は，黒潮系暖水分布域が陸棚斜面付近および九州沿岸へと縮小する傾向となることであり，冬期との相違が明瞭であることが分かった．

3．九州西岸域での黒潮系暖水の変動傾向

九州西岸沖合域に分布する黒潮系暖水の変動は，九州西岸沿岸域での海況変動に大きな影響を及ぼすことは明らかであり，黒潮系暖水分布域の経年変動に見られる特徴を把握しておくことは重要である．そこで，黒潮系暖水分布域の月毎の指標水温を定め，分布域の経年変動を検討した．

黒潮系暖水分布域の経年変動を調べるために，月毎の黒潮系暖水指標水温を設定し，設定した水温の等温線が32° Nと交差する経度を東シナ海海況速報（漁業情報サービスセンター）から読み取り，その位置を黒潮系暖水分布域の境界として東西変動を調べた．なお，読み取った資料は1986年4月～1996年3月の資料である．まず，指標水温は，冬期における黒潮系暖水の北限が32° Nであることから，32° Nの緯線上での冬期，夏期の黒潮系暖水分布域の西端であるW，S（Fig. 1）での平年値をもとに，月毎の指標水温を設定した（Table 1)．3，4節では冬期を10～3月，夏期を6～9月と定義したが，4，5月については，長江流量が年間平均値を下回ることから大陸沿岸水の影響は少ないものとして，本報告では冬期として取り扱うこととする．すなわち，10～5月はWでの平年値を，また6～9月はSでの平年値を指標水温として用いた．なお，指標水温は小数点以下を四捨五入した．

Fig. 8 に月毎の平年位置および分散を示す．冬期（10～5月）の平均位置は127° 20′ E付近に見られた．さらに平年位置からの分散も3月を除いて小さく，冬期の黒潮系暖水の分布域は，ほぼ安定していたことが分かる．反対に，6～9月にかけては平年位置が大き

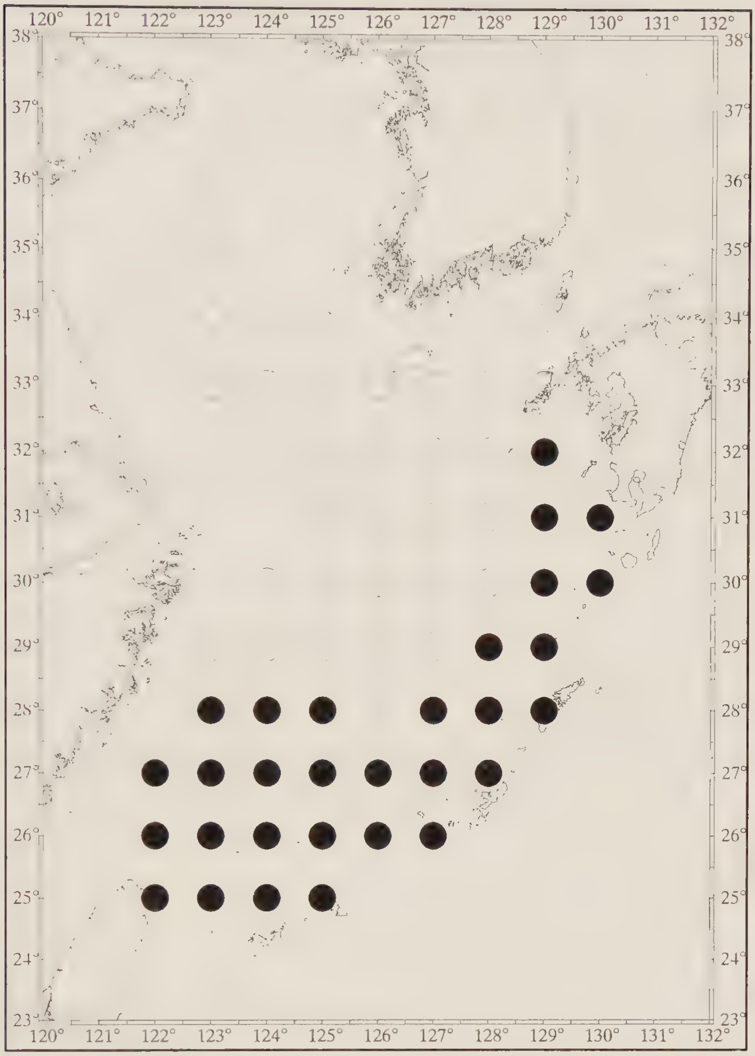


Fig. 7. An average year water mass distributions in summer in the East China Sea. White circles denote the continental coastal water grids and solid circles denote the Kuroshio water grids.

Table 1. Monthly index temperature of the Kuroshio water west of Kyushu Island obtained by annually mean temperature at W (from November to May) and S (from June to October) in Fig. 1.

Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
18℃	16℃	16℃	17℃	18℃	23℃	26℃	28℃	27℃	25℃	22℃	20℃

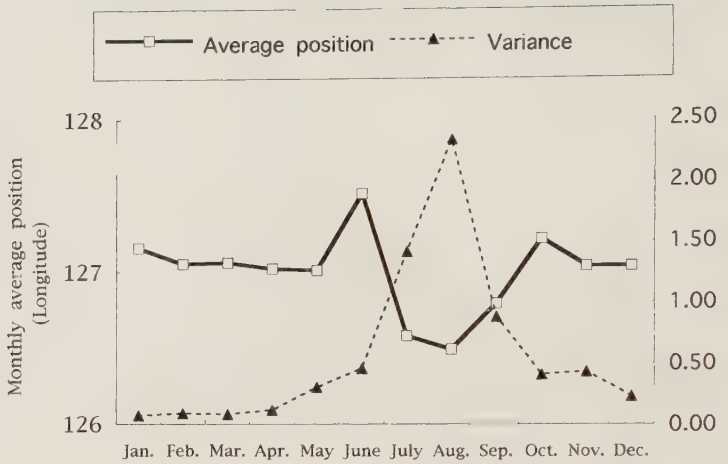


Fig. 8. The average year position (□) of the Kuroshio water and its variance (▲).



Fig. 9. The annual changes (1986–1997) of both the deviation from the average year position (solid line) and 13-months running mean values (dotted line).

く変動し，6月には127°30′Eへと東偏し，7～9月には126°30′Eへと西偏する．特に8月には平年位置からの分散が著しく大きな値を示すことから，位置変動が極めて大きいことが分かる．これは夏期における大陸沿岸水の分布面積が長江の流量に比例し，夏期の長江流量変動が極めて大きいことに起因するものと考えられる（井上，1981；皆川，1997）．

次に経年変動の特徴を詳細に見るために，平年位置からの偏差を月毎に求め Fig. 9 に示した．太線で示した13カ月間の移動平均値を見ると，1987年から徐々に西偏傾向が強まったことが分かる．さらに詳しく調べるために13カ月間での移動平均値を用いて自己相関関数を求めた（Fig. 10）．これによると27カ月のラグタイムにピークが現われており，黒潮系暖水分布域の経年変動には，ほぼ2.25年の周期性を認めることができた．金子ら（1987）は東シナ海表面水温に見られる2年周期帯のパワー分布および台湾東方の水温を基準としたコヒーレンスや位相のずれの分布から，黄海から舌状にのびる沿岸水の先端部で2年周期の変動が大きく現われ，この変動は黒潮からの変動の伝幡を示唆

するものと報告している．さらに1930年代以降，東シナ海表面水温の経年変動に，２～３年（これらをまとめて準２年周期変動と呼ばれている）の周期性が定常的に認められ，冬期の季節風の吹き出しとの関連が指摘されている（Watanabe et. al., 1986）．以上のことから九州西方の黒潮系暖水の分布域は黒潮，大気さらには長江流量の複合的な影響を受けて経年的に変動するものと考えられた．今後，上記の各変動要素が黒潮系暖水分布域の変動に与える影響をさらに吟味し，定量化して行く必要がある．

ま　と　め

東シナ海での冬期および夏期における平年的な水塊分布図を作成した．その結果から，1）冬期には黒潮分派の東側（宮古島北方）では黄海冷水の分布域が27°Nまで南下し，黒潮系暖水分布域は男女群島付近（32°N，128°E）へと西方に張り出す，2）夏期には台湾北東方に台湾暖流によるものと考えられる黒潮系暖水が認められ，九州西方の黒潮系暖水の分布域は冬期に比べて九州西岸方向へと縮小することが分かった．

黒潮分派について，井上（1981）は黄海冷水の南下に伴う補流であり，冬期の季節風の吹き出しに対応して流速が増加するとしている．一方，潘ら（1990）は台湾海峡から北東方向に流れる台湾暖流が夏期に強勢となり黒潮分派分布域が縮小すると推察しており，今後，黒潮分派と台湾暖流との識別を行なうことが重要な課題である．

また，九州西岸での黒潮系暖水の平年位置および平年位置からの分散より，平年位置は冬期を通じてほぼ安定していたことが分かった．しかし夏期（７～９月）には分散が著しく大きな値を示すことから，年変動が極めて大きいことが分かった．夏期に示される大きな年変動は，長江流量変動が夏期に極めて大きく，大陸沿岸水の分布面積が長江の流量に比例することに起因するものと考えられる．

さらに，九州西方での黒潮系暖水分布域の東西変動には，2.25年の周期性を認めることができた．このことは，春季，九州西岸域に産卵場を形成する魚類の行動に影響を与える海洋環境変動，特に水温変動が10年周期で繰り返される傾向があることを示唆するものである．今後，黒潮系暖水分布域変動が漁況変動に与える影響については，より長期的な対応関係を調査する必要がある．



Fig. 10 The autocorrelation function calculated from 13-month running mean values of the deviation from the average year position.

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Behavioral Response of Sharks to Electric Stimulation

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ABSTRACT

The behavioral responses of sharks to electric stimulation were studied. We used two methods of electric stimulation, one is the Electric Field Experiment (EFE) and the other is the Partial Electric Field Experiment (PEF). The responses of three species of sharks, *Carcharhinus falciformis* (60 cm TL), *Triaenodon obesus* (119 cm TL), and *Stegostoma fasciatum* (220 cm TL), to the EFE electric stimulation were studied. The captive sharks swam in a circular tank (7 m in diameter, 1.2 m in depth). The source unit consisted of a signal generator, which produced the wave form, frequency, and voltage, and a power amplifier. Electrodes were 5 cm×10 cm copper plates, separated by a distance of 3.5 m. A 60 Hz sine wave and DC pulse electric fields were chosen. The 60 Hz sine wave was 1 V to 10 V (r.m.s) and the DC pulse period was either 1 sec or 5 sec (duty ratio is 10%). All sharks swam close to the side of the tank when the signal generator was off. When the 60 Hz sine wave and DC pulse electric field were being produced, two species, *C. falciformis* and *T. obesus*, immediately turned around. The sharks were demonstrated a high rate of turning when exposed to the DC pulse electric fields. Conversely, *S. fasciatum* did not change its swimming patterns when the signal generator was on.

The PEF was conducted for eight species; three species were same the individuals tested in the EFE plus five additional species: *Galeocerdo cuvier* (218 cm TL),

Received January 14, 2000（平成12年1月14日受理）
Contribution from Seikai National Fisheries Research Institute, No. 597（西海区水産研究所業績第597号）

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Carcharhinus melanopterus (65 cm TL), *Triakis scyllium* (64 cm TL), *Cephaloscyllium isabellum* (53 cm TL), and *Scyliorhinus torazame* (42 cm TL). Electrodes were separated by a distance of 30 cm or 2 cm. Four species, *C. melanopterus*, *C. falciformis*, *T. obesus*, and *T. scyllium*, gave a strong response to the electric field, two species, *C. isabellum* and *S. torazame*, gave a weak response to the electric field, but two other species, *G. cuvier* and *S. fasciatum*, did not show a response to the electric field. Hence, the behavioral response patterns were different among the species.

Objectives of the study include the results of the behavioral responses of sharks to electric stimulation and examination of the possibility of electric fields for repellence from shark attacks and protection from shark depredation of fisheries.

INTRODUCTION

Elasmobranch fishes respond to weak electrical voltage gradients, which they detect with the ampullae of Lorenzini (Kalmijin, 1978). Dijkgraaf and Kalmijin (1962) found that skates could detect voltage gradients as low as 0.01 microvolts per centimeter. Kalmijin (1971) reported that the shark, *Scyliorhinus canicula*, and the skate, *Raja clavata*, are extremely sensitive to weak electric fields and they can be stimulated by the bioelectric fields emanating from the flatfish. Kalmijin (1978) demonstrated that the bottom dwelling, shallow-water shark, *Mustelus canis*, the common smooth dogfish, can detect minute electrical voltage gradients as small as five thousandths of a microvolt (=5 nanovolts) per centimeter. Understanding the shark's mechanoreceptive sense is easy compared with grasping the nature of their "sixth sense", the ability to sense weak electric fields (Hueter and Gilbert, 1990). Sharks not only sense these fields but also rely upon them to locate prey and perhaps navigate through the ocean (Hueter and Gilbert, 1990). Tricas et al. (1995) reported that the weak stimulus is used in the field by reproductively active male stingrays to locate mates, and also by female rays to locate buried consexuals. Sisneros et al. (1998) stated that reproductively active adult clearnose skates discharge their electric organs at rates near the peak frequency sensitivity of the adult electrosensory system, which facilitates electric communication during social behavior.

In addition to feeding and reproductive studies, electric fields have been studied as a methods of repellence from shark attack. The electric dart is an experimental weapon that can instantly paralyze a large shark (Nelson, 1983). The expendable dart (which remains on the shark) is delivered by spear and

produces a pulsed electric field between the inside of the shark and the outside water (Baldridge, 1974; Nelson, 1983). Electric shark barriers were arranged around beaches in South Africa to prevent sharks from entering thus protecting bathers (Smith, 1991). The Natal Sharks Board, South Africa, developed the "Shark POD" (Shark Protective Oceanic Device) in 1992 (Taylor, 1998). The Shark POD used an electric field to protect divers and not injure the shark (Taylor, 1998). However, differences in behavioral response of several shark species to the electric field are not clearly described.

A fatal shark attack on a shell diver occurred in Aichi Prefecture on 9 April 1995 (Yano, 1996a, b). The Aichi Prefecture Government started a shark research project to study attacks and the behavior of sharks. Our project team studied the behavioral response of sharks to several electric stimuli. We used two methods of electric stimulation, one is the Electric Field Experiment (EFE) and the other is the Partial Electric Field Experiment (PEF).

Objectives of the study include 1) the results of the behavioral responses of sharks to electric stimulation and 2) examination of the possibility of electric fields for repellence from shark attacks and protection from shark depredation of fisheries.

MATERIALS AND METHODS

Electric Field Experiment (EFE)

The sharks used in the electric field experiment are listed in Table 1. We tested the behavioral response of three species; the silky shark, *Carcharhinus*

Table 1. The sharks used in the Electric Field Experiment (EFE), Partial Electric Field Experiment with electrodes separated by a distance of 30 cm (PEF-30), and PEF with electrodes separated by a distance of 2 cm (PEF-2).

Species name	Total length (cm)	Sex	Number of experiment		
			EFE	PEF-30	PEF-2
Carcharhinus falciformis	60	female	23	5	0
Triaenodon obesus	119	male	7	5	0
Stegostoma fasciatum	220	female	3	5	0
Galeocerdo cuvier	218	female	0	6	0
Carcharhinus melanopterus	65	male	0	0	5
Triakis scyllium	64	female	0	0	5
Cepahloscyllium isabellum	53	female	0	0	5
Scyliorhinus torazame	42	male	0	0	5

falciformis, the whitetip reef shark, *Triaenodon obesus*, and the zebra shark, *Stegostoma fasciatum*. One individual swam in the tank during each experiment. The number of experiments ranged from three to 23 for each species (Table 1).

The methods used in the EFE are outlined in Fig. 1. The captive sharks swam in a circular tank, 7 m in diameter and 1.2 m in depth, at the Okinawa Expo Aquarium. We conducted the electric field experiment from 11 to 13 December, 1996. The electric source unit consisted of a signal generator (Yokokawa Denki FG 120) and power amplifier (NF Kairo 4502). The signal generator produced the wave form, frequency, and voltage. A 60 Hz sine wave and DC pulse electric fields were chosen. The 60 Hz sine wave was 1 V to 10 V (r.m.s) and 0.1 A to 2.5 A, and the DC pulse was 0.2 V to 10 V and 0.1 A to 5 A. The pulse period for experiment No. 9 was 0.5 seconds of stimulation and 4.5 seconds without stimulation (duty ratio is 10%) and experiment No. 19 was 0.1 seconds of stimulation and 1.9 seconds without stimulation (duty ratio is 10%) (Table 2). All other experiments were 0.1 seconds of stimulation and 0.9 seconds without stimulation (duty ratio is 10%), for 10 minutes (Table 2).

Electrodes were 5 cm by 10 cm copper plates, separated by a distance of 3.5 m. We set one of the electrodes at the center of the tank and set the other electrode on the side of the tank (Fig. 1). We observed swimming patterns during normal conditions and while presenting electric stimuli to the sharks for 10 minutes and recorded the patterns with two video cameras from different angles. One camera

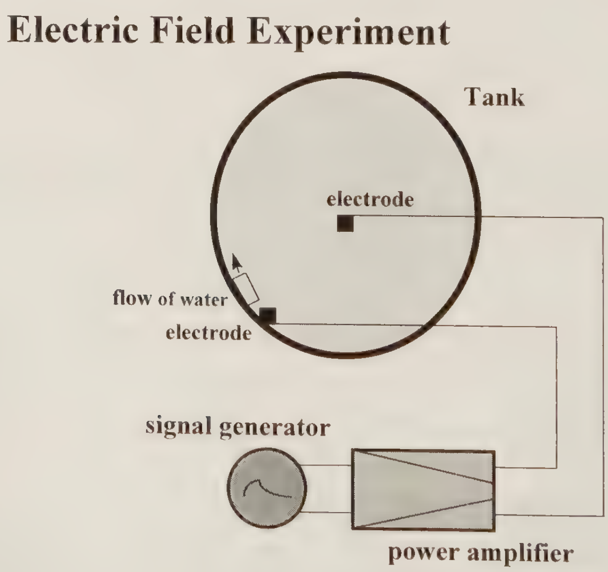


Fig. 1. Outline of the methods for the Electric Field Experiment (EFE).

Table 2. Date and time of experiments, type of stimulation, number of turns, number of passes between electrodes, and behavioral response during EFE of three species of sharks, *Carcharhinus falciformis*, *Triaenodon obesus*, and *Stegostoma fasciatum*. ++ : very strong response ; + : strong response ; − : no response.

Number of experiment	Date of experiment	Time of experiment	Type of stimulation	Electric current (A)	Potential difference (V)	Pulse period for stimulation (sec)	Pulse period for no stimulation (sec)	Number of turns	Number of passes between electrodes	Response
C. faciformis										
1	11 Dec 96	13:20–13:30	No					1	22	−
2	11 Dec 96	13:35–13:45	DC pulse	5	10	0.1	0.9	40	15	++
3	11 Dec 96	14:07–14:17	No					2	17	−
4	11 Dec 96	14:20–14:30	60Hz sine	2.5	10			11	13	+
5	11 Dec 96	14:51–15:01	No					1	21	−
6	11 Dec 96	15:05–15:15	DC pulse	5	10	0.1	0.9	41	16	++
7	11 Dec 96	15:39–15:49	No					0	22	−
8	11 Dec 96	15:50–16:00	60Hz sine	1.95	3.75			7	20	+
9	11 Dec 96	16:23–16:33	DC pulse	5	10	0.5	4.5	13	25	++
10	12 Dec 96	10:38–10:48	No					2	15	
11	12 Dec 96	10:52–11:02	DC pulse	0.5	1	0.1	0.9	46	3	++
12	12 Dec 96	11:37–11:47	No					1	18	−
13	12 Dec 96	11:49–11:59	DC pulse	0.1	0.2	0.1	0.9	42	1	++
14	12 Dec 96	12:10–12:20	No					1	16	
15	12 Dec 96	12:24–12:34	No					4	20	
16	12 Dec 96	12:36–12:46	60Hz sine	0.1	1			1	21	+
17	12 Dec 96	14:00–14:10	60Hz sine	0.6	1.5			2	23	+
18	12 Dec 96	14:13–14:23	No					0	24	−
19	12 Dec 96	14:25–14:35	DC pulse	0.1	0.2	0.1	1.9	103	12	++
20	12 Dec 96	14:55–15:05	DC pulse	0.1	0.2	0.1	0.9	42	4	++
21	12 Dec 96	15:21–15:31	No					0	22	
22	12 Dec 96	15:34–15:44	DC pulse	0.1	0.2	0.1	0.9	71	3	++
23	12 Dec 96	15:52–16:02	DC pulse	1	10	0.1	0.9	59	2	++
S. fasciatum										
24	13 Dec 96	10:41–10:51	No					0	28	−
25	13 Dec 96	10:54–11:04	60Hz sine	0.68	5			0	30	−
26	13 Dec 96	11:15–11:25	DC pulse	10	7	0.1	0.9	0	30	−
T. obesus										
27	13 Dec 96	14:15–14:25	No					1	14	−
28	13 Dec 96	14:28–14:38	DC pulse	1	0.2	0.1	0.9	44	22	++
29	13 Dec 96	14:49–14:59	No					2	11	−
30	13 Dec 96	15:02–15:12	DC pulse	1	1	0.1	0.9	71	9	++
31	13 Dec 96	15:29–15:39	DC pulse	1	7	0.1	0.9	52	5	++
32	13 Dec 96	16:04–16:14	No					3	22	
33	13 Dec 96	16:18–16:28	60Hz sine	1	5			45	4	+

recorded the whole tank and the other followed the swimming positions of the shark. We measured the swimming patterns of the sharks for 10 minutes, when the electric source unit was on, and then with no electric stimulation for at least 30 minutes until the next experiment. The number of turns and the number of passes between the electrodes were counted from the video tape recordings after the experiments.

We used field mapping methods (0.675 A, 60 Hz, 34 per mil sea waters) to measure the intensity of the electric field. The field mapping measurement points were 1 cm interval within the limits (17 cm × 12 cm). The intensity of the electric field around the electrodes was high but the intensity between the electrodes was low (Fig. 2A).

Partial Electric Field Experiment (PEF)

The methods used in the PEF are outlined in Fig. 3. The electric source unit

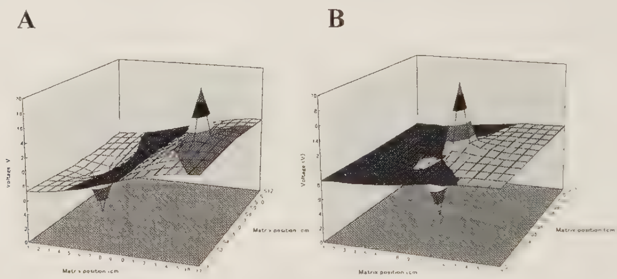


Fig. 2. The model of intensity slope of the electric field around the electrodes measured by field mapping methods. A: Electric Field Experiment (0.675 A, 60 Hz, 34 per mil); B: Partial Electric Field Experiment (1.03 A, 60 Hz, 34 per mil).

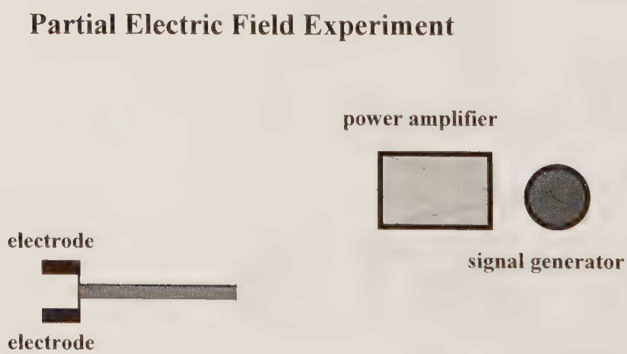


Fig. 3. Outline of the methods for the Partial Electric Field Experiment (PEF).

was the same as used in the EFE. Electrodes were separated by a distance of 30 cm or 2 cm. The 50 Hz or 60 Hz sine waves were 10 V (r.m.s.) and 2.0 A and 2.5 A, the DC pulse was 1 V to 10 V and 0.05 A to 5 A, and the pulse period was 0.1 seconds of stimulation and 0.9 seconds without stimulation (duty ratio is 10%).

The intensity of the electric field in the small area around the electrodes was high but the intensity between electrodes was low, measured by field mapping methods (1.03 A, 60 Hz, 34 per mil sea water) (Fig. 2B). The filed mapping measurement points were 1 cm interval within the limits (17 cm × 14 cm).

The sharks tested in the PEF are listed in Table 2. In the experiments, four species, the silky shark, *C. falciformis*, the whitetip reef shark, *T. obesus*, the zebra shark, *S. fasciatum*, and the tiger shark, *Galeocerdo cuvier*, were tested with electrodes (5 cm × 10 cm) separated by a distance of 30 cm. These sharks were tested from 10 to 15 December, 1996 in a circular tank (7 m in diameter and 1.2 m in depth) at the Okinawa Expo Aquarium (Fig. 4A). The other four species, the blacktip reef shark, *Carcharhinus melanopterus*, the banded houndshark, *Triakis scyllium*, the swell shark, *Cephaloscyllium isabellum*, and the cloudy catshark, *Scyliorhinus torazame*, were tested with electrodes (1 cm in diameter) separated by a distance of 2 cm. These sharks were tested from 26 to 28 February, 1996 in a transportation tank (180 cm × 120 cm, 70 cm deep) at the Hekinan Seaside Aquarium (Fig. 4B).

The electrodes for PEF were not at fixed location in the tank because a pole with the electrodes could be moved around in the tank. The near the snout region of the sharks was approached with the dipole electrodes (Fig. 4). We tested each PEF experiment 5 or 6 times and then with no electric stimulation for at least 20 minutes until the next experiment. We recorded the swimming behavior of the shark with a video camera when the electric source unit was on and off.

RESULTS

Electric Field Experiment (EFE)

Carcharhinus falciformis

The tracks of the swimming patterns of the silky shark, *C. falciformis*, with no electric stimulation, with a 60 Hz sine wave stimulation, and a DC pulse stimulation are shown in Fig. 5. The shark swam close to the side of the tank and passed between the electrodes when the electric source unit was off (Fig. 5A). When the 60 Hz sine wave electric fields were being produced, the shark passed almost in the center between the electrodes (Fig. 5B). When the DC pulse electric fields were being produced, the shark immediately turned around (Fig. 6) and rarely passed

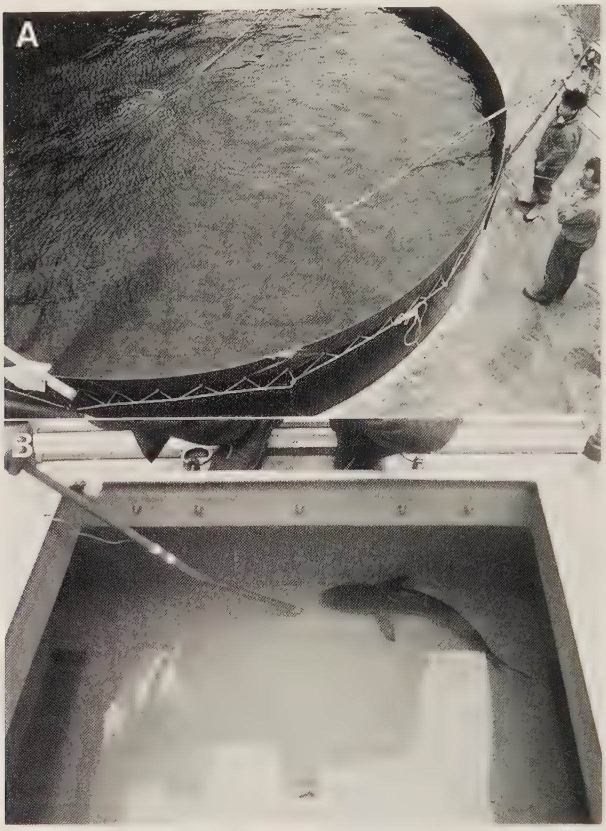


Fig. 4. The snout region of the tiger shark, *Galeocerdo cuvier* (A) and the blacktip reef shark, *Carcharhinus melanopterus* (B) were approached with the dipole electrodes.



Fig. 5. The tracks of the swimming patterns of the silky shark, *Carcharhinus falciformis*. A: no stimulation (normal); B: 60 Hz sine wave electric field; C: DC pulse electric field.

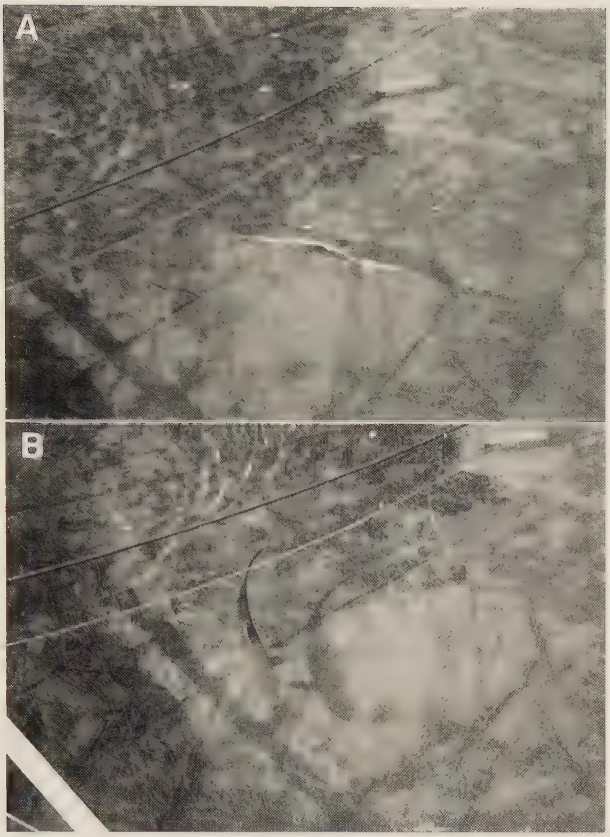


Fig. 6. The silky shark, *Carcharhinus falciformis*, immediately turned around in front of the electrodes (E) when the DC pulse electric fields were being produced by the EFE. A : no stimulation (normal) ; B : DC pulse electric stimulation, the shark immediately turned around.

between the electrodes (Fig. 5C, Table 2). The shark shook its head very strongly right and left when the DC pulse electric fields were being produced at all the time and all the position in the tank. Twenty-three experiments with this species resulted in similar swimming patterns with the normal, the 60 Hz sine wave and the DC pulse stimulation. When the electric source unit was off, the shark returned quickly to a normal swimming pattern.

The number of turns made by the silky shark during 10 minutes is shown in Tables 2 and 3. An average of 50.8 turns were observed during the DC pulse electric stimulation. The number of turns during the DC pulse electric stimulation was clearly higher than that of the normal swimming condition. The 60 Hz sine wave electric stimulation and normal conditions produced few turns by the shark.

Table 3. The number of turns made by three species, *Carcharhinus falciformis*, *Triaenodon obesus*, and *Stegostoma fasciatum*, exposed to the EFE.

Species name	No electric stimulation				DC pulse stimulation				60 Hz sine wave stimulation			
	average	range	SD	n	average	range	SD	n	average	range	SD	n
Carcharhinus falciformis	1.2	0–4	1.22	10	50.78	13–103	25.05	9	5.25	1–11	4.65	4
Triaenodon obesus	2	1–3	1	3	55.67	44–71	13.87	3	45	—	—	1
Stegostoma fasciatum	0	—	—	1	0	—	—	1	0	—	—	1

Table 4. The number of passes between the electrodes by three species, *Carcharhinus falciformis*, *Triaenodon obesus*, and *Stegostoma fasciatum*, exposed to the EFE.

Species name	No electric stimulation				DC pulse stimulation				60 Hz sine wave stimulation			
	average	range	SD	n	average	range	SD	n	average	range	SD	n
Carcharhinus falciformis	19.7	15–24	3.02	10	9.0	1–25	8.37	9	19.3	13–23	4.35	4
Triaenodon obesus	15.7	11–22	5.69	3	12.0	5–22	8.89	3	4	—	—	1
Stegostoma fasciatum	28	—	—	1	30	—	—	1	30	—	—	1

There are 5.3 on average for the 60 Hz sine wave electric stimulation and 1.2 for normal conditions (Table 3). The number of turns was not significantly different between the 60 Hz sine wave electric stimulation and the normal condition (Mann–Whitney U–test, $U_{(4, 10)}=7.0$, 2 tie, $P=0.058$).

The number of passes between the electrodes by the silky shark in 10 minutes is shown in Tables 2 and 4. The numbers of passes between the electrodes averaged 9.0 for the DC pulse electric stimulation, 19.3 for the 60 Hz sine wave electric stimulation, and 19.7 for the normal condition (Table 4). The number of passes between the electrodes was significantly different between the DC pulse electric stimulation and the normal condition (Mann–Whitney U–test, $U_{(9, 10)}=12$, 2 tie, $P=0.007$). The number of turns for the DC pulse electric stimulation was lower than those of the 60 Hz sine wave electric stimulation and the normal swimming condition of the shark. The number of passes between the electrodes was not significantly different between the 60 Hz sine wave electric stimulation and the normal condition (Mann–Whitney U–test, $U_{(4, 10)}=19.0$, 2 tie, $P=0.867$).

The number of turns in each experiment of the DC pulse stimulation with the silky shark is shown in Fig. 7A. When the electric current was low, many turns were observed.

The number of passes between the electrodes during each experiment of the DC pulse stimulation with the silky shark is shown in Fig. 7B. When the electric current was high, many passes were made between the electrodes. A higher electric field does not always result in a greater behavioral response by the shark.

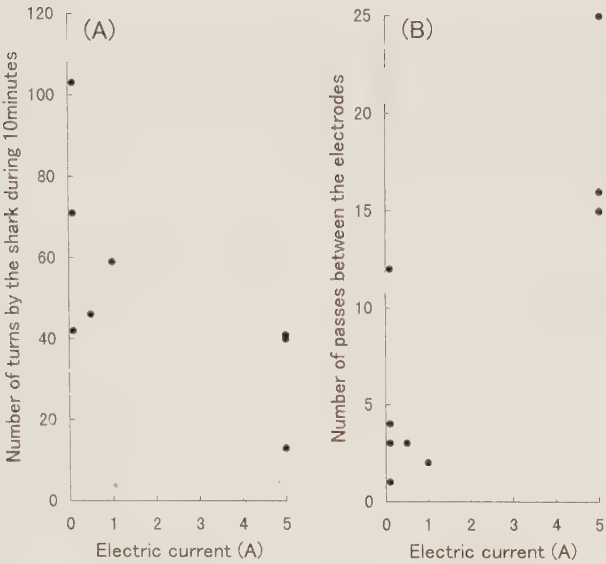


Fig. 7. The number of turns in each experiment (A) and the number of passes between the electrodes during each experiment (B) with the silky shark, *Carcharhinus falciformis*.



Fig. 8. The tracks of the swimming patterns of the whitetip reef shark, *Triaenodon obesus*. A: no stimulation (normal); B: 60 Hz sine wave electric field; C: DC pulse electric field.

Triaenodon obesus.

The tracks of the swimming patterns of the whitetip reef shark, *T. obesus*, with no electric stimulation, with a 60 Hz sine wave stimulation, and a DC pulse stimulation are shown in Fig. 8. The shark swam close to the side of the tank and passed between the electrodes when the electric source unit was off (Fig. 8A). When the 60 Hz sine wave electric fields were being produced, the shark immediately turned around, passed a few times between the electrodes and swam far away from the electrodes (Fig. 8B). When the DC pulse electric fields were being produced, the shark immediately turned around, but the shark passed between the electrodes (Fig. 8C). The shark strongly shook its head right and left when

exposed to both the 60 Hz sine wave electric stimulation and the DC pulse electric stimulation were being produced at all the time and all the position in the tank. However the head shaking of the silky shark was stronger than that of the whitetip reef shark. When the electric source unit was off, the shark quickly returned to a normal swimming pattern.

The whitetip reef shark averaged 55.7 turns during the DC pulse electric stimulation, 45 for the 60 Hz sine wave electric stimulation, and 2.0 during the normal condition (Tables 2 and 3). The number of turns was significantly different between the DC pulse electric stimulation and the normal condition (Mann–Whitney U–test, $U_{(3,3)}=0$, $P=0.05$). The number of turns of the 60 Hz sine wave was also clearly different from that of the normal condition. Many turns by the shark were observed during the DC pulse electric stimulation and the 60 Hz sine wave electric stimulation. Normal swimming of the shark included very few turns.

In the whitetip reef shark, the number of passes between the electrodes averaged 12 for the DC pulse electric stimulation, 4 for the 60 Hz sine wave electric stimulation and 15.7 for the normal swimming condition (Table 4). The number of passes between the electrodes during the DC pulse and the 60 Hz sine wave electric stimulation was lower than during normal swimming. However, the number of passes between the electrodes was not significantly different between the DC pulse electric stimulation and the normal condition (Mann–Whitney U–test, $U_{(3,3)}=2.5$, 1 tie, $P=0.37$). The number of passes through the 60 Hz sine wave was clearly fewer than that of the normal condition (Table 4).

Stegostoma fasciatum.

The tracks of the swimming patterns of the zebra shark, *S. fasciatum*, with no electric stimulation, with a 60 Hz sine wave stimulation, and a DC pulse stimulation are shown in Fig. 9. In contrast to the other two, this species did not change its



Fig. 9. The tracks of the swimming patterns of the zebra shark, *Stegostoma faciatum*. A: no stimulation (normal); B: 60 Hz sine wave electric field; C: DC pulse electric field.

swimming patterns when the electric source unit was on (Fig. 9B, C). The zebra shark did not turn around during the DC pulse stimulation, the 60 Hz sine wave stimulation, or the normal condition (Tables 2 and 3). The number of passes of the zebra shark did not differ between the normal condition and the electric stimulation by the DC pulse and the 60 Hz sine wave (Tables 2 and 4).

Partial Electric Field Experiment (PEF)

The behavioral responses of the sharks during the PEF are shown in Table 5. Four species, the silky shark, *C. falciformis*, the whitetip reef shark, *T. obesus*, the blacktip reef shark, *C. melanopterus*, and the banded houndshark, *T. scyllium*, showed a strong response to the electric field, swimming very fast and sometimes bumping the wall of the tank. The sharks attempted to escape from the electrodes when the electric source unit was on (Table 5). The swell shark, *C. isabellum*, and the cloudy catshark, *S. torazame*, did not show a response to a 5 mA electric stimulation. However they showed a weak response (their head moved only slightly) to a 400 mA electric stimulation (Table 5). The sharks did not attempt to escape from the electrodes when the electric source unit was on. Two other species, the zebra shark, *S. fasciatum*, and the tiger shark, *G. cuvier*, did not show a response to the electric field (Table 5). Their swimming speeds and direction of the swimming course did not change when they were exposed to the electric field. The behavioral response patterns were thus different among the species.

DISCUSSION

Elasmobranchs are known to respond to weak electrical stimulation (Kalmijin, 1971, 1974, 1978; Ryan, 1981). In behavioral tests, sharks and skates appeared most responsive to frequencies in the range from 0 (direct current) to about 8 Hz (Kalmijin, 1971, 1974). Sisneros et al. (1998) reported that best frequency of clearnose skate (*Raja eglanteria*) was at 1–2 Hz for embryos, showed an upwards shift to 5 Hz in juveniles, an a downward shift to 2–3 Hz in adults. The receptors detecting these weak, low-frequency electric fields are the ampullae of Lorenzini, delicate sensory structures in the elasmobranch's protruding snouts (Murray, 1962; Dijkgraaf and Kalmijin, 1963). The ampullae of Lorenzini of elasmobranchs are sensitive to weak electrical fields produced by the nerves and muscles of other animals (Kalmijin, 1971, 1978). On the other hand, electric stimulation in the present study repelled several sharks.

In the EFE and the PEF, the silky shark, the whitetip reef shark, the blacktip reef shark, and the banded houndshark attempted to escape from the electric fields.

Table 5. Behavioral response during the PEF of eight species of sharks. ++ : strong response; + : weak response; − : no response.

Species name	Electrode distance	Stimulation	Electric current	Potential difference	Response
Carcharhinus falciformis	30	No			−
	30	60 Hz sine	2.5 A	10 V	++
	30	DC pulse	1.25 A	7 V	++
	30	DC pulse	820 mA	5 V	++
	30	DC pulse	147 mA	1 V	++
Triaenodon obesus	30	No			−
	30	60 Hz sine	2.5 A	10 V	++
	30	DC pulse	1.25 A	7 V	++
	30	DC pulse	820 mA	5 V	++
	30	DC pulse	147 mA	1 V	++
Stegostoma fasciatum	30	No			−
	30	60 Hz sine	2.5 A	10 V	−
	30	DC pulse	1.25 A	7 V	−
	30	DC pulse	820 mA	5 V	−
	30	DC pulse	147 mA	1 V	−
Galeocerdo cuvier	30	No			−
	30	60 Hz sine	2.5 A	10 V	−
	30	DC pulse	5 A	10 V	−
	30	DC pulse	1.25 A	7 V	−
	30	DC pulse	820 mA	5 V	−
	30	DC pulse	147 mA	1 V	−
Carcharhinus melanopterus	2	No			−
	2	50 Hz sine	2.0 A	10 V	++
	2	DC pulse	700 mA	5 V	++
	2	DC pulse	400 mA	5 V	++
	2	DC pulse	5 mA	1 V	++
Triakis scyllium	2	No			−
	2	50 Hz sine	2.0 A	10 V	++
	2	DC pulse	700 mA	5 V	++
	2	DC pulse	400 mA	5 V	++
	2	DC pulse	5 mA	1 V	++
Cepahloscyllium isabellum	2	No			−
	2	50 Hz sine	2.0 A	10 V	−
	2	DC pulse	700 mA	5 V	+
	2	DC pulse	400 mA	5 V	+
	2	DC pulse	5 mA	1 V	−
Scyliorhinus torazame	2	No			−
	2	50 Hz sine	2.0 A	10 V	−
	2	DC pulse	700 mA	5 V	+
	2	DC pulse	400 mA	5 V	+
	2	DC pulse	5 mA	1 V	−

It is suggested that the sharks have an aversion to the electric fields used in our experiments. Elasmobranchs use weak bioelectric fields emanating from prey animals, but the stimulation of our experiments is probably stronger than any naturally encountered electric stimulus. We think that the sharks were not able to tolerate the stimulation. During the EFE, the silky shark and the whitetip reef shark passed almost in the center between the electrodes. Field mapping of the intensity of the electric field (Fig. 2) suggests that the center intensity between the electrodes has the lowest electric field. We think that the shark may sense the lower electric field in the center and pass through there.

Devices using electric fields have been developed for protection against shark attacks, for example, the electric dart (Baldridge, 1974), electric shark barrier (Smith, 1991), and the Shark POD (Taylor, 1998). Baldridge (1974) reported that by using a pulsed stimulus of only about 20–30 V, breadboard models of the electric antishark dart have been very successful. He reported that a tiger shark was paralyzed immediately, however, much work remains to be done in miniaturizing the power supply and circuitry and perfecting the delivery system before such weapons could be made generally available to divers. The Shark POD was measured to pulse an electric potential of ±30 V and 60 V in potential difference (in air) (Fukui et al., 1997). This electric potential (60 V) of the Shark POD is 6 to 300 times higher than in our experiments (0.2–10 V). Our findings suggest that a lower electric potentials are useful for shark repellents. However, the behavioral response patterns were different among the species.

In the EFE, dramatic responses to the electric filed were observed in the silky shark and the whitetip reef shark. No responses to the electric field were observed with the zebra shark. In the PEF, large responses to the electric field were observed in the silky shark, the whitetip reef shark, the blacktip reef shark, and the banded houndshark. But four other species, the zebra shark, the tiger shark, the swell shark, and the cloudy catshark did not change their swimming pattern or responded only weakly to the electric field. The behavioral response patterns also differed with the intensity and kind of electric field among the species in the present study. For example, the silky shark responded more strongly to the DC pulse electric stimulation than the 60 Hz sine wave electric stimulation, but the whitetip reef shark showed a stronger response to the 60 Hz sine wave electric stimulation than the DC pulse electric stimulation. Thus, we think that the behavioral response patterns of each species are related to the wave form, frequency, and voltage of the electric fields. Baldridge (1974) reported that a tiger shark was paralyzed immediately by a 20–30 V pulse stimulus. However, in our experiments the tiger shark did not respond to the electric field. Our electric stimulation was

lower than Baldridge's stimulation. We think that the tiger shark responds to a higher electric field than the electric field used in our experiments.

Strong responses to an electric field are documented for the dusky shark, *Carcharhinus obscurus*, the bull shark, *C. leucas*, and the white shark, *Carcharodon carcharias* (Smith, 1991; Taylor, 1998). Hence, we think that an electric field is a useful method for protection from some species during shark attacks. However, the electric field seems to have little effect once the sharks start to feed. Taylor (1998) reported that during the Shark POD test, tiger shark, *G. cuvier*, lemon shark, *Negaprion acutidens*, great hammerhead, *Sphyrna mokarran*, whaler, *Carcharhinus amblyrhyncos*, and tawny shark, *Nebrius ferrugineus* came to the bait. She stated that these experiments reinforced her feeling that once a shark starts eating, the desire to feed overrides the instinct of self preservation. Further studies are needed to determine conclusively whether these reactions are different by species and wave form, frequency and voltage of the electric field.

In line fisheries, longlines, drop lines, and rod and reel, depredation of catch fishes by sharks has been documented (Sivasubramanium, 1965; Hirayama, 1976; Kobayashi and Yamaguchi, 1978; Yano, 1996b). Hirayama (1976) reported that the depredation rate of tuna longlines by sharks was calculated to range between 1.64–14.45% of the tuna catch. Kobayashi and Yamaguchi(1978) reported that the depredation rate of tuna longlines by sharks was estimated to be up to 7.5% of the total catch. In the Ryukyu Islands, high depredation of the catch by sharks is known in bottom drop lines and rod and reel fisheries (Yano, 1998, 1999). In particular areas around the islands depredation rates by sharks were estimated of 10 to 30% of the total catch (Yano, unpublished). In those areas, several species of *Carcharhinus* and *G. cuvier* are mainly observed to depredate catch fishes (Yano, 1998). Several species of *Carcharhinus* were observed to respond to electric fields by previous researchers and the present study. Taylor (1998) reported that the big Queensland grouper, *Epinephelus lanceolatus*, was unaffected by electric stimulation. If teleost fishes are unaffected by electric stimulation, the development electric field generating equipment for use on fishing gear may decrease the depredation rate of the catch fishes by sharks. For example, electrodes attached to the line gear could pulse electric fields around the hooks.

ACKNOWLEDGMENTS

We thank H. Mizuno, E. Fukui, K. Terada, S. Iwata, and K. Nakano and the Aichi Prefecture Government, for their support of the research fund and help with the experiments; to the staff members of the Okinawa Expo Aquarium, the

Hekinan Seaside Aquarium, and the Aichi Fisheries Research Institute, and the students of the Institute of Medical Electronics, University of Tokyo, for their assistance with the experiments; to S. Kajiura and A. Bush, at the Hawaii Institute of Marine Biology, for their valuable advice and review of the manuscript.

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電気刺激に対するサメ類の反応実験

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抄　　録

電界印加実験および局部電界発生実験（電撃実験）を用いて，電気刺激に対するサメ類の反応について研究を行った．

電界印加実験（EFE）は，クロトガリザメ，ネムリブカ，トラフザメの3種類で行った．実験方法は，直径7メートルの円形水槽の中心部と縁辺部に銅板電極を設置し，電流を流して実験魚の遊泳行動の観察を行った．実験は方形波パルスと 60Hz 正弦波交流を電力増幅し，電極間に印加した．電界印加実験は1回の実験につき10分間行い，ビデオカメラによる撮影と目視による行動観察を行った．3種類の実験魚の通常の遊泳行動は，円形水槽の縁に沿って遊泳していた．クロトガリザメとネムリブカは，電界印加を与えたところ，頭部を左右に振り急激な方向変換をし，その回数は通常の遊泳行動よりも多かった．そして，電極付近には近づかず，電極間もほとんど通過することがなく，これら2種は電界を嫌う行動がみられた．一方，トラフザメは電界印可を行っても遊泳行動に変化が現れることがなかった．

局部電界発生実験（PEF）は，EFE の実験魚3種とイタチザメについては円形水槽で，ツマグロ，ドチザメ，ナヌカザメ，トラザメでは長方形水槽（180cm×120cm×70cm）で実験を行った．クロトガリザメ，ツマグロ，ネムリブカ，ドチザメは，電撃刺激に対して非常に強い逃避行動の反応がみられた．ナヌカザメとトラザメでは，電撃刺激に対して頭部をほんの僅か振る程度の非常に弱い反応があり，逃避行動もみられなかった．イタチザメとトラフザメは電撃刺激に対してまったく反応しなかった．

以上のように電気刺激に対して非常に強い逃避行動がみられる種類もいるが，まったく反応しない種類もみられ，これら刺激に対する反応には種類別に違いがあることが判明した．そのため，電気刺激に対する反応が強い種類では，サメ類の人的被害防止あるいは漁業への食害防止のために電気刺激を利用できることが示唆された．

Species Composition of Epifauna and Infauna on Intertidal Boulder Shores at Ishigaki Island in Subtropical Japan

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ABSTRACT

Species compositions of intertidal epifauna and infauna were quantitatively investigated on boulder shores at Ishigaki Island in subtropical Japan. These faunae were collected by quadrat for 4～5 seasons×3 shores×5～6 heights. In total, 112 species in epifauna and 27 species in infauna were collected. Among epifauna, species number was higher in mobile animals (97 species) than in sessile ones (15 species). Among the mobile animals, species number was highest in Gastropoda (68 species), in which *Nerita squamulata* was abundant (the highest density for each shore: 50.0 to 500.0 m^{-2}). Among the sessile animals, however, species number was highest in Bivalvia (14 species). Among infauna, species number was highest in Bivalvia (26 species) which abundantly included *Asaphis violascens* (the highest density for each shore: 12.0 to 83.0 m^{-2}) and *Ruditapes variegatus* (5.6 to 26.0 m^{-2}), holding edible molluscs as many as 10 species. The species composition of these faunae varied 1) among shores, more sharply for epifauna than for infauna; 2) among seasons, sharply for both faunae on some shores; and 3) among heights, sharply for both faunae. Such variations in species composition and the rareness of sessile species are discussed in relation to unique environments of boulder shores.

INTRODUCTION

Intertidal boulder shores often consist of boulders and sandy sediment, which harbor epifauna and infauna, respectively. These faunae are often unique, not found for rocky or sandy shores (Kubo and Kurozumi, 1995). Their species com-

Received January 19, 2000 (平成12年1月19日受理)
Contribution from Seikai National Fisheries Research Institute, No. 598 (西海区水産研究所業績第598号)
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positions have seldom been quantitatively studied, except the surveys on epifauna in eastern Australia (McGuinness, 1987) and in western Japan (Takada and Kikuchi, 1990; 1991).

These epifauna and infauna are important as fishery resources and also as materials for ecological study. Some of them such as turban snails and clams are well consumed by local people (Kubo and Kurozumi, 1995). The boulder shore faunae show unique ecological features regarding morphology (Takada, 1992), population dynamics (Kurihara et al., in preparation), and community structure (McGuinness, 1987), not found for rocky or sandy shore faunae (e.g. Takada, 1996; McGuinness, 1987).

In the present study, the species compositions of both epifauna and infauna were seasonally investigated at several heights on several intertidal boulder shores at Ishigaki Island in subtropical Japan. On these boulder shores, the abundance of only epifauna in a season was previously reported (Nishihira, 1975). However, not only epifauna but also infauna should be studied, because they are also important fishery resources and have unique ecological characteristics not found in epifauna (e.g., Kurihara et al., in preparation). In addition, their species compositions should be seasonally studied, considering that the species compositions are likely to differ between seasons; this is because various environmental factors (e.g. desiccation, boulder cover rate), which may affect the population dynamics of each species, vary seasonally. For both epifauna and infauna, we showed differences in species composition among shores, among seasons and among heights. We also listed edible species and presented a paucity of sessile species.

METHODS

Boulder shores at Ishigaki Island in subtropical Japan (Fig. 1) were investigated at Ibaruma (Shore A; 124°17′E, 24°30′N), Ohta (Shore B; 124°14′E, 24°27′N) and Sakieda (Shore C; 124°07′E, 24°25′N). On each shore, boulders (mean ±SD diameter=34.7±21.9 mm; N=1336) were distributed with vertical range being 15–50 m and horizontal range being 50–100 m. They made 1–2 layers upon sandy sediment. In this sandy sediment, boulders of approximately the same size also occurred. Tides were semidiurnal, showing a mean range of 1.6 m from lower low water to higher high water at spring tide. Surface seawater temperature was lowest in February 1998 (23.0℃) and highest in August 1998 (34.1℃). Mean±SE wave height at low tide was 4.0±1.2 cm (Shore A), 7.7±1.7 cm (Shore B) and 4.8±0.7 cm (Shore C).

On these shores, seasonal sampling was conducted at spring tides for 4 or 5



Fig. 1. Map of the study sites

dates×5 or 6 heights×4 quadrats. Shores B and C were investigated in September 1997, December 1997, March 1998, June 1998 and September 1998. Simultaneously Shore A was observed except September 1997. Such deficiency for Shore A was due to the construction of a dike. Transects of 12.8, 47.5 and 21.7 m lengths were determined for Shores A, B and C, respectively. The vertical ranges of these transects from a base line (defined as the mean sea level minus 1.0 m) were 0.44 to 1.53 m (Shore A), 0.41 to 1.10 m (Shore B) and 0.23 to 0.90 m (Shore C). In each transect, 5 heights (Shores A and C) or 6 heights (Shore B) were determined. At each height, 4 quadrats were arranged at approximately 1 m intervals without

overlap during the present study. The size of the quadrat was generally 0.5×0.5 m^2, but occasionally 0.3×0.3 m^2 at the lowest and second lowest heights on Shore B when too many epibenthos occurred.

Inside the quadrat, all epifauna (approximately >1 mm) was collected by turning over boulders. Then infauna at 0–10 cm depths in sandy sediment was sampled with a 6×6 mm^2–mesh sieve. Of these faunae, Polychaeta, Diogenidae, Insecta, Phascolosoma, Polyplacophora and Sipunculoidea were excluded due to difficulties with species identification. We also excluded the gastropods *Clypeomorus batillariaeformis* and *C. bifasciata* that were < 10 mm in shell height, because these were apt to be confused with each other.

The remainders were categorized and analyzed in the following way. The animals sold around Ishigaki Island were defined as edible species (Table 1). The animals attaching to boulders (e.g. barnacles and mussels) were defined as sessile species. The ratio of sessile species number to all epifauna species number for the present study was compared with the values for previous studies on intertidal boulder or rocky shores. The previous studies referred were such that both species name and sediment type were properly described (Underwood, 1981; Lubchenco *et al.*, 1984; Mori *et al.*, 1985; McGuinness and Underwood, 1986; Ohgaki *et al.*, 1997; Dye, 1988).

RESULTS

In total, 22115 individuals in 139 species were collected (Table 1; see Suppl–table 1 for detailed data). Of these, 20628 individuals in 112 species were epifauna, mainly consisting of Gastropoda (68 species) and Crustacea (26 sp.). The remainder was infauna (1476 individuals in 27 species), mainly consisting of Bivalvia (26 sp.) with edible molluscs as many as 10 species (Table 1). In epifauna, the ratio of sessile species number to all species number was lower for the present study (13.3%) than for previous studies (30.8 to 40.2%; Table 2).

The ratio of a species density to the total density of all species ("relative abundance", hereafter) was calculated for the 5 most dominant species in each fauna on each shore (Table 3). It differed among shores for epifauna more markedly than for infauna. That is, dominant species commonly found for every shore was only one in epifauna (gastropod *Nerita squamulata*), while being two in infauna (bivalves *Asaphis violascens* and *Ruditapes variegatus*). Additionally, dominant species common to two arbitrarily–chosen shores was none in epifauna, while being two in infauna (bivalves *Coecella chinensis* and *Gafrarium tumidum*).

Seasonal variation in these patterns was presented in Fig. 2. For each season,

Table 1. The number of individuals for each species and shore.
The species were typed as edible one (e), sessile one(s) or neither (blank).

Fauna	Class	Order	Family	Species: Latin name	Species: Japanese name	Type	Shore A	Shore B	Shore C
Epifauna									
	Gastropoda								
		Patellogastropoda							
			Lottiidae	*Patelloida striata*	Ryukyuaogai		54	764	38
		Archaeogastropoda							
			Acmaeidae	*Patelloida pygmaea*	Himekozaragai		98	18	50
			Fissurellidae	*Emarginula variegta*	Susuirosusokiregai			26	6
			Neritidae	*Clithon faba*	Kanokogai			104	
				Clithon chlorostoma	Hanagasumikanokogai			56	
				Nerita albicilla	Amaobune		2		34
				Nerita chamaeleon	Oomaruamaobune			1	
				Nerita helicinoides	Ishidatamiamaobune		42		
				Nerita insculpta	Ryukyuamagai		20		
				Nerita plicata	Kibaamagai		5		
				Nerita polita	Nishikiamaobune		1		1
				Nerita bensoni	Ukonnamagai			4	1
				Nerita squamulata	Maruamaobune		217	5269	228
				Nerita striata	Koshidakaamagai		4		
			Trochidae	*Monodonta labio*	Okinawaishidatami		42	169	114
				Tectus maculatus	Nishikiuzugai				1
			Liotiidae	*Liotina peroni*	Ryukyuhimekatabe				1
			Turbinidae	*Collonista costulosa*	Murasakisannsyousugai				2
				Lunella granulata	Kanngiku	e	34	32	277
				Stomatella phymotis	Huruyagai				1
		Archaeotaenioglossa							
			Truncatellidae	*Truncatella guerinii*	Kubikiregai		358		
			Thiaridae	*Thiara granifera*	Iboayakawanina				1
		Neotaenioglossa							
			Cerithidae	*Clypeomorus batillariaeformis*	Umininakanimori		1		2605
				Clypeomorus bifasciata	Kayanomikanimori		7		200
				Clypeomorus irrorata	Semushitsunobue		23		29
				Clypeomorus subbrevicula	Ooshimakanimori			7687	32
				Plesiotrochus acutangulus	Chigusakanimori				4
				Plesiotrochus parcus	Ooshimachigusakanimori				1
				Rhinoclavis vertagus	Takenokokanimori				2
			Littorinidae	*Littoraria intermedia*	Himeuzuratamakibi		1		
				Littoraria scabra	Uzuratamakibi		7		
				Littoraria undulata	Hososujiuzuratamakibi		1		
				Peasiella conoidalis	Hinanourauzu		1		
			Planaxidae	*Angiola inepta*	Yokosujitamakibigaimodoki			1	
				Planaxis sulcatus	Gomahunina		594		29
			Strombidae	*Strombus urceus*	Ohagurogai				3
			Cypraeidae	*Cypraea annulus*	Hanabiradakara				18
				Cypraea errones	Natsumedakaramodoki				1
				Cypraea moneta	Kiirodakara				1
			Naticidae	*Natica fasciata*	Kuchigurotamagai				7
				Natica gualtieriana	Housyunotamagai			7	5
				Polinices pyryformis	Rouirotomigai				1
			Ranellidae	*Cymatium nicobaricm*	Mitsukadobora				2
			Assimineidae	*Angustassiminea castanea*	Kuriirokawazannsyougai		512		
		Neogastropoda							
			Muricidae	*Muricodrupa fusca*	Reishigaidamashimodoki			56	14
				Cronia fiscella	Yourakureishigaidamashi			1	2
				Cronia margariticola	Unereishigaidamashi			3	165
				Morula anaxeres	Uneshiroreishigaidamashi				20
				Morula granulata	Reishigaidamashi				4
				Thais pseudodiadema	Ohaguroreishigai			11	1
				Thais squamosa	Koiwanishi				1
			Buccinidae	*Japeuthria cingulata*	Shimabekkoubai			27	1
				Nassarius coronatus	Iboyoubai				2
				Nassarius semisulcatus	Atsumushirogai			7	33
				Nassarius velatum	Shiinomiyoubai				1
				Pusiostoma mendricaria	Noshigai				1
			Mitridae	*Pterygia dactylus*	Imohude				3
			Costellariidae	*Vexillum balteolatum*	Minomushigai				3
				Vexillum grueneri	Haiirominomushigai				1
				Vexillum michaui	Konntsukushigai				1
				Vexillum rugosum	Shiwaminomushigai				13
			Turridae	*Clavus unizonaris*	Hitosujitsunokudamaki				1
			Conidae	*Conus cornatus*	Juzukakesayagataimogai				1
				Conus ebraeus	Madaraimogai				2
		Heterobranchia							
			Pyramidellidae	*Otopleura glans*	Susogurokuchikiregai			1	
			Oncidiidae	*Onchidium verruculatum*	Isoawamochi				2
			Siphonariidae	*Siphonaridae laciniosa*	Koudakakaramatsugai				28
			Ellobiidae	*Melampus castaneus*	Hamashiinomigai		29		

Table 1. (Continued)

Fauna	Class	Order	Family	Species: Latin name	Species: Japanese name	Type	Shore A	Shore B	Shore C
Epifauna									
	Bivalvia								
		Arcoida							
			Arcidae	*Barbatia amygdalumtortum*	Beniegai	S			3
				Barbatia cruciata	Kurominoegai	S			1
				Barbatia virescens	Kariganeegai	S	6		8
				Striarca symmetrica	Mimiegai	S			3
		Mytiloida							
			Mytilidae	*Hormomya mutabilis*	Hibarigaimodoki	S	1	1	
				Modiolus auriculatus	Ryukyuhibarigai	S			5
		Pterioida							
			Pteriidae	*Pinctada maculata*	Midoriaorigai	S		1	1
			Isognomonidae	*Isognomon legumen*	Shiroaorigai	S	6		
				Isognomon nucleus	Heritoriaorigai	S	10		
				Isognomon pernum	Kaishiaorigai	S			57
		Veneroida							
			Lasaeidae	*Lionelita denticulata*	Kizamishitatarigai	S		1	
			Chamidae	*Chama iostoma*	Kanetsukezarugai	S			18
			Kelliidae	*Pythina deshayeiana*	Sewakehachimitsugai	S		1	
			Carditidae	*Cardita leana*	Tomayagai	S			1
	Maxillopoda								
		Sessilia							
			Balanidae	*Balanus albicostatus*	Shirosujihujitsubo	S	3		
	Crustacea								
		Decapoda							
			Leucosiidae	*Leucosia perlata*	Hutamekobushigani		1		1
				Oreophorus latusoides	Tsunokaruishikobushi				2
				Philyura taekoae	Amamimamekobushigani			3	4
			Majidae	*Micippa philyra*	Kowatakuzugani				1
			Parthenopidae	*Parthenope calappoides*	Abatahishigani				1
			Thiidae	*Kraussia rugulosa*	Shiwagoishigani				9
				Kraussia truncatifrons	Hutabagoishigani				2
			Portunidae	*Portunus bidens*	Sagamihimegazami				1
				Thalamita crenata	Minamibenitsukegani		1		
				Thalamita prymma	Benitsukegani		1		4
			Xanthidae	*Actumnus setifer*	Suehiroibotegani				7
				Cyclograpsus intermedius	Akaisogani		7		
				Epixanthus frontalis	Sebiroougigani		6		
				Pilumnus uespertilio	Kebukagani				3
			Grapsidae	*Cyclograpsus integer*	Minamiakaisogani		1		
				Gaetice depressus	Hiraisogani		17	16	
				Helice leachi	Minamiashiharagani		7		
				Nanosesarma gordoni	Himebennkeigani				1
				Pachygrapsus mimutus	Himeiwagani		1	1	1
				Pseudograpsus elongatus	Kounagaiwaganimodoki		7	17	4
			Mictyridae	*Mictyris brevidactylus*	Minamikometsukigani		1		
			Ocypodidae	*Macrophthalmus serenei*	Menagaosagani		3		23
				Macrophthalmus bosci	Himekakuosagani				6
				Uca perplexa	Okinawahakusennshiomaneki		1		2
				Uca tetragonon	Rurimadarashiomaneki				1
			Coenobitidae	*Coenobita cavipes*	Okayadokari		1	11	
	Ophiuroidea								
		Myophiurida							
			Ophiocomidae	*Ophiocoma dentata*	Gomahukumohitode				14
			Ophiodermatidae	*Ophiarachnella infernalis*	Minamiitsutsumekumohitode				17
	Holothuroidea								
		Aspidochirotida							
			Holothuriidae	*Holothuria leucospilota*	Nisekuronamako				2
Infauna									
	Bivalvia								
		Arcoida							
			Arcidae	*Anadara antiquata*	Ryukyusarubougai	e			2
		Veneroida							
			Lucinidae	*Anodontia edentula*	Kaburatsukigai				1
				Epicodakia divergens	Himetsukigai			1	
				Pillucina pisidium	Umenohanagai				5
			Galeommatidae	*Pseudegaleomma rosea*	Barairomameagemakigai				2
			Mactridae	*Meropesta cuneata*	Tamamaki		1		
			Mesodesmatidae	*Atactodea striata*	Isohamaguri	e	1	11	35
				Coecella chinensis	Kuchibagai	e	76	18	10
				Davila plana	Naminokomasuogai		3		
			Tellinidae	*Exotica transculpta*	Hasumezakuragai				18
				Loxoglypta compta	Mikunishiborizakuragai				1
				Pinguitellina pinguis	Migakihimezaragai				2
				Quadrans gurgadia	Ootogeunegai				1
				Semelangulus tokubei	Komezakura				1
				Tellina staurella	Himenikkougai				8
			Psammobiidae	*Asaphis violascens*	Ryukyumasuogai		539	51	257
				Psammotaea elongata	Masuogai	e		127	
			Semelidae	*Semele carnicolor*	Samezaragaimodoki	e			21
			Donacidae	*Donax faba*	Ryukyunaminokogai	e		14	5
			Veneridae	*Gafrarium pectinatum*	Hososujiinamigai				16
				Gafrarium tumidum	Arasujikemann	e	6	1	51
				Irus mitis	Matsukaze				1
				Katelysia hiantina	Yaeyamasudarehamaguri	e	7		
				Pitar citrinum	Yuukagehamaguri				4
				Ruditapes variegatus	Himeasari	e	14	42	121
				Tapes literatus	Ryukyuasari	e			1
	Echiuroidea								
			Thalassemidae	*Ochetostoma erythrogrammon*	Sujiyumushi			1	

Table 2. Ratio of sessile species number to total epifauna species number.

Reference	Study site	Substrate	Total species number	Ratio of sessile species (%)
The present study	Ishigaki Island (124° E, 24° N)	Boulders on sandy sediments	113	13.3
Underwood (1981; page 64)	Sydney (151° E, 34° S)	Rocky platform	19	31.6
Lubchenco *et al*. (1984; p62–65)	Bay of Panama (79° W, 8° N)	Rocky platform	73	35.6
Mori *et al*. (1985; p30)	China Sea coast of Japan (130° E, 32° N)	Rocky platform	20	40.0
McGuinness and Underwood (1986; p107)	Sydney (151° E, 34° S)	Boulders on rocky platform	57	40.2
Ohgaki *et al*. (1997; p101)	Pacific coast of central Japan (135° E, 33° N)	Rocky platform	52	30.8
Dye (1998; p288)	Pacific coast of South Africa (29° E, 32° S)	Rocky platform	18	33.3

Table 3. Relative abundance (i.e., the ratio of a species density to the total epifauna species densities) for dominant species on each shore.

	Shore	Total number of specimens	Species	Relative abundance (%)
Epifauna	A	3503	*Planaxis sulcatus*	27.3
			Angustassiminea castanea	23.5
			Truncatella guerinii	16.5
			Nerita squamulata	10.0
			Patelloida pygmaea	4.5
			Others	18.2
	B	10852	*Clypeomorus subbrevicula*	50.9
			Nerita squamulata	39.6
			Patelloida striata	5.6
			Monodonta labio	0.7
			Clithon faba	0.6
			Others	2.6
	C	4743	*Clypeomorus batillariaeformis*	64.0
			Lunella granulata	6.3
			Nerita squamulata	5.0
			Cronia margariticola	4.0
			Clypeomorus bifasciata	2.9
			Others	17.8
Infauna	A	914	*Asaphis violascens*	82.0
			Coecella chinensis	11.6
			Ruditapes variegatus	2.1
			Katelysia hiantina	1.1
			Gafrarium tumidum	0.9
			Others	2.3
	B	273	*Psammotaea elongata*	57.6
			Ruditapes variegatus	14.5
			Asaphis violascens	12.2
			Coecella chinensis	4.2
			Donax faba	3.3
			Others	8.1
	C	779	*Asaphis violascens*	44.2
			Ruditapes variegatus	19.7
			Atactodea striata	7.3
			Gafrarium tumidum	6.9
			Exotica transculpta	3.4
			Others	18.5

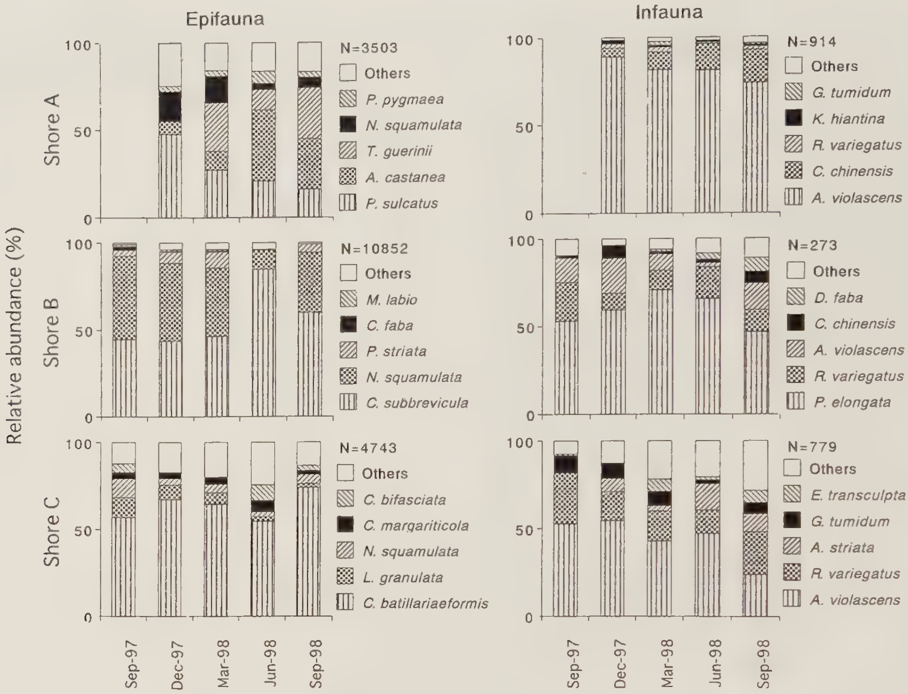


Fig. 2. Seasonal change in relative abundance (i.e., the ratio of a species density to total epifauna species densities) presented for 5 most dominant species on each shore. No sampling was made for September 1997 on Shore A due to the construction of a dike.

N. squamulata (the highest density for each shore: 50.0 to 500.0 m^{-2}) in epifauna, and *A. violascens* (12.0 to 83.0 m^{2}) and *R. variegatus* (5.6 to 26.0 m^{-2}) in infauna were abundantly collected on each shore (Suppl–table 1). For epifauna, dominant species seasonally changed their relative abundances clearly for Shores A and B. That is, for Shore A the relative abuncances of *Planaxis sulcatus* and *Angustassiminea castanea* seasonally fluctuated with the range of >30%, and for Shore B the relative abundances of *C. subbrevicula* and *N. squamulata* varied with the range of >35%. For infauna, however, such seasonal fluctuation was greater for Shore C where *A. violascens* relative abundance ranged from 24 to 54%.

Vertical change in relative abundance was remarkable except epifauna on Shore B (Fig. e). That is, for epifauna (Shores A and C) and infauna (all shores), neither the most dominant species nor the second one was common between the highest and lowest heights.

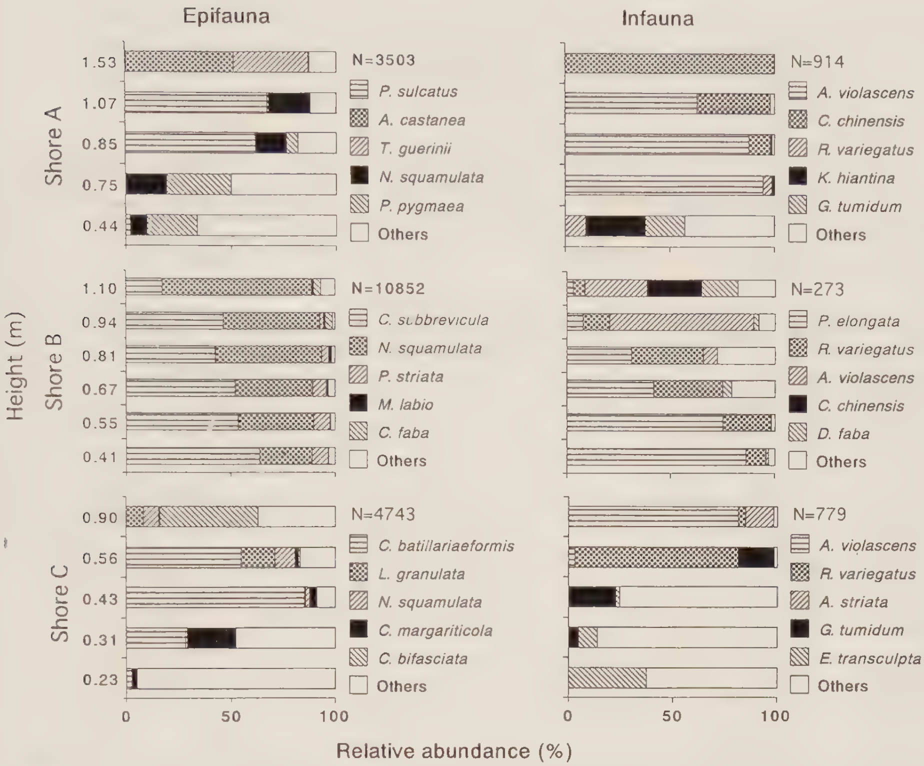


Fig. 3. Vertical change in relative abundance of dominant species. For detail, see the caption of Fig. 2.

DISCUSSION

Among–shore difference in species composition was greater for epifauna than for infauna (Table 3). This might be because among–shore difference in environmental factors may more markedly affect epifauna species composition than infauna species composition. For example, the amount of sandy sediment, being transported from river to intertidal boulder shores, differs among shores (Kurihara *et al.*, in preparation) ; such among–shore difference in sandy sediment can change more remarkably epifauna species composition than infauna species composition. This is because the sandy sediment appears to disturb epifauna more greatly than infauna (Kurihara *et al.*, in preparation). In addition to such sediment disturbance, the other environmental factors such as wave action (see Methods) and desiccation (Kurihara *et al.*, in preparation) vary among shores, which may alter epifauna species composition more conspicuously than infauna species composition. This is

Suppl-table 1. Mean±SE density (m^{-2}) of each species for each season and height. (A) Shore A, (B) Shore B, (C) Shore C. Species are divided into families by lines. Blank denotes that no speciemen was collected.

(A) Shore A

Species		Dec 1997					Mar 1998				
Latin name	Japanese name	1.53m	1.07m	0.85m	0.75m	0.44m	1.53m	1.07m	0.85m	0.75m	0.44m
Patelloida striata	Ryukyuaogai				29.0 + 11.8					9.0±4.1	
Patelloida pygmaea	Himekozaragai			3.0±3.0	13.0 ±4.7			1.0±1.0		16.0±7.1	
Nerita albicilla	Amaobune										
Nerita helicinoides	Ishidatamiamaobune		1.0±1.0				4.0±4.0	10.0±10.0			
Nerita insculpta	Ryukyuamagai	4.0±2.8					2.0±2.0				
Nerita plicata	Kibaamagai										
Nerita polita	Nishikiamaobune										
Nerita squamulata	Maruamaobune	2.0±2.0	51.0±19.7	13.0±6.4	13.0±7.9			54.0±10.9	21.0±12.8	11.0±1.9	1.0±1.0
Nerita striata	Koshidakaamagai		4.0±2.8								
Monodonta labio	Okinawaishidatami		17.0±1.9	3.0±3.0	2.0±1.2			6.0±3.5	1.0±1.0	3.0±3.0	
Lunella granulata	Kanngiku			11.0±7.2	4.0±2.8				2.0±2.0	6.0±2.0	2.0±2.0
Truncatella guerinii	Kubikiregai	4.0±2.3					154.0±92.5				
Clypeomorus batillariaeformis	Umininakanimori										
Clypeomorus bifasciata	Kayanomikanimori									3.0±1.9	
Clypeomorus irrorata	Semushitsunobue			2.0±2.0					4.0±4.0	9.0±4.1	
Littoraria intermedia	Himeuzuratamakibi							1.0±1.0			
Littoraria scabra	Uzuratamakibi										
Littoraria undulata	Hososujiuzuratamakibi						1.0±1.0				
Peasiella conoidalis	Hinanourauzu										
Planaxis sulcatus	Gomahunina		175.0±72.7	51.0±49.7				54.0 + 34.8	96.0±75.7		1.0±1.0
Angustassiminea castanea	Kuriirokawazannsyougai	35.0±7.5					61.0±34.5				
Melampus castaneus	Hamashiinomigai						12.0±5.9				
Barbatia virescens	Kariganeegai										
Hormomya mutabilis	Hibarigaimodoki										
Isognomon legumen	Shiroaorigai			6.0±6.0							
Isognomon nucleus	Heritoriaorigai										
Balanus albicostatus	Shirosujihujitsubo										
Leucosia perlata	Hutamekobushigani					1.0±1.0					
Thalamita crenata	Minamibenitsukegani										
Thalamita prymma	Benitsukegani										1.0±1.0
Cyclograpsus intermedius	Akaisogani	3.0±1.9						1.0±1.0			
Epixanthus frontalis	Sebiroougigani	2.0±2.0						3.0±1.9			
Cyclograpsus integer	Minamiakaisogani	1.0±1.0									
Gaetice depressus	Hiraisogani										
Helice leachi	Minamiashiharagani	5.0±3.8					1.0±1.0		1.0±1.0		
Pachygrapsus mimutus	Himeiwagani										
Pseudograpsus elongatus	Kounagaiwaganimodoki	4.0±1.6									
Mictyris brevidactylus	Minamikometsukigani										
Macrophthalmus serenei	Menagaosagani										
Uca perplexa	Okinawahakusennshiomaneki										
Coenobita cavipes	Okayadokari										
Meropesta cuneata	Tamamaki										1.0±1.0
Atactodea striata	Isohamaguri										1.0±1.0
Coecella chinensis	Kuchibagai	1.0±1.0	10.0±6.6					2.0±1.2	13.0±13.0		
Davila plana	Naminokomasuogai										
Asaphis violascens	Ryukyumasuogai		41.0±13.8	77.0±15.9	68.0 + 12.3			15.0±5.0	44.0±16.3	58.0±12.9	
Gafrarium tumidum	Arasujikemann					1.0±1.0					3.0±3.0
Katelysia hiantina	Yaeyamasudarehamaguri				1.0±1.0	3.0±1.0					1.0±1.0
Ruditapes variegatus	Himeasari			1.0±1.0	4.0±1.6					3.0±1.9	1.0±1.0

because the epifauna, not surrounded and protected by sandy sediment as the infauna, appears to be exposed to such factors more severely.

Although species composition differed among shores (Table 3), the gastropod *N. squamulata* and the bivalves *A. violascens* and *R. variegatus* were constantly abundant on each shore. On every shore, they were abundant for each season and several heights (Figs. 2 and 3). Their dominance is also reported for the other boulder shores around the study sites (Nishihira, 1975; Kubo and Kurozumi, 1995). Such dominance might be related to their possible fecundity; their fecundity is conjectured from their shell size frequency data, in which recruitment appears to occur several times in a year (Kurihara, in preparation).

The ratio of sessile species number to total epifauna species number was lower for the present study than for any previous studies (Table 2). Such rarity might

(A) Shore A (continued)

Species	Jun 1998					Sep 1998				
	1.53m	1.07m	0.85m	0.75m	0.44m	1.53m	1.07m	0.85m	0.75m	0.44m
P. striata			5.0±3.8	5.0±5.0	3.0±3.0			1.0±1.0	1.0±1.0	1.0±1.0
P. pygmaea		1.0±1.0	5.0±3.8	34.0±16.4	11.0±11.0			9.0±6.6	4.0±2.3	1.0±1.0
N. albicilla				1.0±1.0					1.0±1.0	
N. helicinoides	3.0±3.0	8.0±6.7				16.0±13.5				
N. insculpta	4.0±1.6					10.0±3.8				
N. plicata	1.0±1.0	1.0±1.0				3.0±1.9				
N. polita		1.0±1.0								
N. squamulata		14.0±8.9	2.0±2.0	8.0±1.6	3.0±1.9	2.0±2.0	4.0±2.8	7.0±3.4	11.0±9.7	
N. striata										
M. labio		4.0±4.0		4.0±4.0				1.0±1.0	1.0±1.0	
L. granulata			1.0±1.0	6.0±3.8	1.0±1.0				1.0±1.0	
T. guerinii	83.0±53.6					117.0±117.0				
C. batillariaeformis									1.0±1.0	
C. bifasciata					4.0±2.8					
C. irrorata				7.0±7.0			1.0±1.0			
L. intermedia										
L. scabra	7.0±4.7									
L. undulata										
P. conoidalis		1.0±1.0								
P. sulcatus		126.0±20.8	26.0±17.9			1.0±1.0	60.0±20.2	4.0±4.0		
A. castanea	300.0±128.1	2.0±1.2				112.0±36.6	2.0±2.0			
M. castaneus	15.0±12.5						1.0±1.0	1.0±1.0		
B. virescens		1.0±1.0	3.0±3.0	1.0±1.0					1.0±1.0	
H. mutabilis									1.0±1.0	
I. legumen										
I. nucleus		4.0±4.0						6.0±3.8		
B. albicostatus									1.0±1.0	2.0±2.0
L. perlata										
T. crenata				1.0±1.0						
T. prymma										
C. intermedius	2.0±1.2					1.0±1.0				
E. frontalis		1.0±1.0								
C. integer										
G. depressus				1.0±1.0						
H. leachi										
P. mimutus							1.0±1.0			
P. elongatus	2.0±2.0		1.0±1.0							
M. brevidactylus					1.0±1.0					
M. serenei					3.0±1.9					
U. perplexa									1.0±1.0	
C. cavipes									1.0±1.0	
M. cuneata										
A. striata										
C. chinensis	1.0±1.0	19.0±6.6	6.0±4.8				22.0±8.9	2.0±2.0		
D. plana										3.0±1.9
A. violascens		19.0±11.8	39.0±14.6	83.0±20.9			21.0±7.7	24.0±5.9	50.0±13.5	
G. tumidum			1.0±1.0						1.0±1.0	
K. hiantina					1.0±1.0					1.0±1.0
R. variegatus				2.0±1.2					2.0±2.0	1.0±1.0

be ascribable to unstable substrates on the present study sites. That is, as above–mentioned, the boulders thereon are often overspread by sandy sediment. Thus, sessile animals adhering to the boulders, which cannot locomote and escape from the sandy sediment, would be subject to higher mortality than mobile animals. This would result in the rarity of sessile animals. Such effects of unstable sediments are also suggested for unstable boulder shores in a main island of Japan (Iijima, personal communication).

Overall, the boulder shore faunae at Ishigaki Island was unique regarding the rareness of sessile species, changing species compositions among shores, seasons and heights except some gastropods and bivalves. The causes are now being experimentally studied (Kurihara, in preparation), especially for the edible molluscs (Table 1). They will be published elsewhere.

(B) Shore B

Species		Sep 1997						Dec 1997					
Latin name	Japanese name	1.10m	0.94m	0.81m	0.67m	0.55m	0.41m	1.10m	0.94m	0.81m	0.67m	0.55m	0.41m
Patelloida striata	Ryukyuaogai		9.0±3.0	18.0±5.3	28.0±9.8	38.9±22.9	19.4±7.0	2.0±1.2	19.0±3.4	39.0±6.4	56.0±11.0	125.0±27.4	66.7±23.6
Patelloida pygmaea	Himekozaragai		1.0±1.0	4.0±2.3	1.0±1.0	2.8±2.8				1.0±1.0	2.0±1.2	8.3±2.8	2.8±2.8
Emarginula variegta	Susuirosusokiregai										4.0±2.8		11.1±4.5
Clithon faba	Kanokogai	19.0±8.1	53.0±16.8	1.0±1.0		2.8±2.8		1.0±1.0	5.0±3.8	2.0±1.2			
Clithon chlorostoma	Hanagasumikanokogai	5.0±3.8						35.0±16.1					
Nerita chamaeleon	Oomaruamaobune												
Nerita helicinoides	Ishidatamiamaobune										1.0±1.0		
Nerita bensoni	Ukonnamagai												
Nerita squamulata	Maruamaobune	123.0±28.4	216.0±52.3	443.0±29.0	300.0±64.4	375.0±178.7	75.0±21.5	264.0±51.0	425.0±4.1	497.0±74.8	258.0±57.9	436.1±93.6	236.1±28.8
Monodonta labio	Okinawaishidatami	1.0±1.0	2.0±1.2	6.0±2.6	3.0±1.0	2.8±2.8		2.0±2.0	21.0±3.0	15.0±6.6	16.0±9.2	2.8±2.8	
Lunella granulata	Kanngiku			1.0±1.0			2.8±2.8		2.0±2.0	4.0±2.3	5.0±1.9	2.8±2.8	5.6±5.6
Clypeomorus subbrevicula	Ooshimakanimori	105.0±36.3	167.0±15.8	202.0±21.6	138.0±45.4	319.4±181.3	500.0±77.5	20.0±6.7	193.0±27.3	98.0±11.1	252.0±174.9	727.8±146.2	763.9±186.1
Angiola inepta	Yokosujitamakibigaimodoki												
Natica gualtieriana	Housyunotamagai				1.0±1.0						1.0±1.0		
Muricodrupa fusca	Reishigaidamashimodoki			2.0±2.0	2.0±2.0				5.0±1.9	6.0±4.8	6.0±3.5	2.8±2.8	8.3±5.3
Cronia fiscella	Yourakureishigaidamashi												
Cronia margariticola	Unereishigaidamashi									1.0±1.0	1.0±1.0		
Thais pseudodiadema	Ohaguroreishigai					5.6±3.2	2.8±2.8					2.8±2.8	2.8±2.8
Japeuthria cingulata	Shimabekkoubai			1.0±1.0	3.0±1.9					2.0±1.2	2.0±1.2	2.8±2.8	2.8±2.8
Nassarius semisulcatus	Atsumushirogai						2.8±2.8				3.0±3.0		2.8±2.8
Otopleura glans	Susogurokuchikiregai												
Hormomya mutabilis	Hibarigaimodoki												
Pinctada maculata	Midoriaorigai												2.8±2.8
Lionelita denticulata	Kizamishitatarigai												
Pythira deshayeiana	Sewakehachimitsugai								1.0±1.0				
Philyura taekoae	Amamimamekobushigani												
Gaetice depressus	Hiraisogani										2.0±1.2		
Pachygrapsus mimutus	Himeiwagani												
Pseudograpsus elongatus	Kounagaiwaganimodoki								1.0±1.0				
Coenobita cavipes	Okayadokari												
Epicodakia divergens	Himetsukigai									1.0±1.0			
Atactodea striata	Isohamaguri												
Coecella chinensis	Kuchibagai	1.0±1.0						6.0±2.6					
Asaphis violascens	Ryukyumasuogai	5.0±3.0	4.0±1.6					3.0±3.0	10.0±3.5				2.8±2.8
Psammotaea elongata	Masuogai		1.0±1.0	2.0±2.0	4.0±2.8	16.7±10.6	11.1±4.5	2.0±2.0			3.0±3.0	8.3±5.3	33.3±33.3
Donax faba	Ryukyunaminokogai												
Gafrarium tumidum	Arasujikemann												
Ruditapes variegatus	Himeasari	1.0±1.0	2.0±2.0	3.0±1.9	3.0±1.9	2.8±2.8	2.8±2.8			2.0±2.0	3.0±3.0		2.8±2.8
Ochetostoma erythrogrammon	Sujiyumushi												

(B) Shore B (continued)

Species	Mar 1998						Jun 1998						Sep 1998					
	1.10m	0.94m	0.81m	0.67m	0.55m	0.41m	1.10m	0.94m	0.81m	0.67m	0.55m	0.41m	1.10m	0.94m	0.81m	0.67m	0.55m	0.41m
P. striata	2.0±2.0	6.0±2.6	34.0±6.2	55.0±15.7	94.4±5.6	100.0±12.0				2.0±2.0				1.0±1.0	1.0±1.0	1.0±1.0	36.1±21.0	116.7±60.3
P. pygmaea				2.0±1.2						2.0±2.0								
E. variegta			1.0±1.0	8.0±0.0	11.1±4.5	11.1±4.5												
C. faba		7.0±5.7	1.0±1.0					4.0±2.8					5.0±5.0					
C. chlorostoma		1.0±1.0						3.0±1.0					4.0±2.3					
N. chamaeleon																		
N. helicinoides																		
N. bensoni			1.0±1.0															
N. squamulata	54.0±52.7	281.0±42.5	254.0±55.5	203.0±34.2	316.7±81.2	133.3±27.6	18.0±18.0	36.0±9.7	53.0±14.8	6.0±4.8		16.7±16.7	105.0±46.9	90.0±42.9	88.0±43.2	118.7±59.0	263.1±140.2	500.0±144.9
M. labio	1.0±1.0	3.0±1.9	8.0±3.7	6.0±2.6	11.1±11.1	5.6±5.6				1.0±1.0			1.0±1.0	1.0±1.0	1.0±1.0			
L. granulata			1.0±1.0	3.0±1.9	8.3±5.3	13.9±13.9				1.0±1.0								
C. subbrevicula		52.0±19.0	231.0±20.7	361.0±59.4	341.7±82.6	463.9±44.1		328.0±92.9	568.0±68.8	47.0±10.0	16.7±7.2	38.9±18.4	13.0±11.7	304.0±205.4	28.0±6.7	418.7±119.0	622.4±216.1	619.4±230.6
A. inepta																		
N. gualtieriana																	1.0±1.0	
M. fusca		2.0±2.0	1.0±1.0	9.0±3.8	11.1±4.5	2.8±2.8			6.0±2.0	1.0±1.0				2.0±2.0				5.6±5.6
C. fiscella						2.8±2.8												
C. margariticola								1.0±1.0										
T. pseudodiadema				1.0±1.0	2.8±2.8							2.8±2.8						2.8±2.8
J. cingulata						5.6±5.6												
N. semisulcatus						2.8±2.8												
O. glans												2.8±2.8						
H. mutabilis									1.0±1.0									
P. maculata																		
L. denticulata			1.0±1.0															
P. deshayeiana																		
P. taekoae												2.8±2.8				2.0±2.0		
G. depressus																		
P. mimutus									1.0±1.0									
P. elongatus		4.0±2.3		1.0±1.0				4.0±0.0					2.0±2.0	1.0±1.0		2.8±2.8		
C. cavipes		1.0±1.0					4.0±2.3						4.0±2.8		1.0±1.0			
E. divergens																		
A. striata	1.0±1.0						1.0±1.0						9.0±5.3					
C. chinensis	1.0±1.0						2.0±2.0						8.0±3.7					
A. violascens		5.0±3.0	1.0±1.0					2.0±1.2					12.0±6.9	6.0±3.8	1.0±1.0			
P. elongata		2.0±1.2	2.0±2.0	1.0±1.0	8.3±5.3	33.3±16.4					2.8±2.8	55.6±29.7			5.0±3.0	2.0±2.0	12.0±7.7	38.9±22.5
D. faba		1.0±1.0					3.0±3.0						9.0±3.8			1.0±1.0		
G. tumidum																	1.0±1.0	
R. variegatus	1.0±1.0		1.0±1.0		2.8±2.8	2.8±2.8		1.0±1.0	3.0±1.0	1.0±1.0	5.6±3.2	5.6±3.2	2.0±1.2	2.0±1.2	1.0±1.0	1.0±1.0	4.0±2.3	5.6±3.2
O. erythrogrammon												2.8±2.8						

(C) Shore C

Species				Sep 1997					Dec 1998		
Latin name	Japanese name	0.90m	0.56m	0.43m	0.31m	0.23m	0.90m	0.56m	0.43m	0.31m	0.23m
Patelloida striata	Ryukyuaogai		5.0±2.5					1.0±1.0			
Patelloida pygmaea	Himekozaragai		3.0±1.9				1.0±1.0	1.0±1.0			
Emarginula variegta	Susuirosusokiregai								1.0±1.0		
Nerita albicilla	Amaobune			1.0±1.0	1.0±1.0				3.0±1.9		
Nerita polita	Nishikiamaobune										
Nerita bensoni	Ukonnamagai										
Nerita squamulata	Maruamaobune	5.0±3.8	50.0±13.1	7.0±2.5				25.0±12.3	3.0±1.0		
Monodonta labio	Okinawaishidatami	10.0±10.(	14.0±5.3				2.0±2.0				
Tectus maculatus	Nishikiuzugai									1.0±1.0	
Liotina peroni	Ryukyuhimekatabe										
Collonista costulosa	Murasakisannsyousugai										
Lunella granulata	Kanngiku	4.0±2.8	66.0±7.6				1.0±1.0	67.0±35.5	2.0±1.2		
Stomatella phymotis	Huruyagai										
Thiara granifera	Iboayakawanina										
Clypeomorus batillariaeformis	Umininakanimori		49.0±37.(	266.0±146.6	26.0±15.7			284.0±41.7	222.0±71.1	45.0±39.7	
Clypeomorus bifasciata	Kayanomikanimori	5.3±0.9	1.3±0.9	0.8±0.8							
Clypeomorus irrorata	Semushitsunobue										
Clypeomorus subbrevicula	Ooshimakanimori										
Plesiotrochus acutangulus	Chigusakanimori								4.0±2.3		
Plesiotrochus parcus	Ooshimachigusakanimori										
Rhinoclavis vertagus	Takenokokanimori								1.0±1.0		
Pianaxis sulcatus	Gomahunina										
Strombus urceus	Ohagurogai										1.0±1.0
Cypraea annulus	Hanabiradakara			1.0+1.0	1.0±1.0	6.0±3.8				2.0±1.2	3.0±1.9
Cypraea errones	Natsumedakaramodoki										
Cypraea moneta	Kiirodakara					1.0±1.0					
Natica fasciata	Kuchigurotamagai									1.0±1.0	2.0±2.0
Natica gualtieriana	Housyunotamagai							1.0±1.0			
Polinices pyryformis	Rouirotomigai										
Cymatium nicobaricm	Mitsukadobora				1.0+1.0					1.0±1.0	
Muricodrupa fusca	Reishigaidamashimodoki		4.0+2.8					2.0±1.2			
Cronia fiscella	Yourakureishigaidamashi										
Cronia margariticola	Unereishigaidamashi	1.0±1.0	3.0±1.9	8.0±2.3	12.0±4.0			12.0±9.5	8.0±1.6	11.0±3.4	1.0±1.0
Morula anaxeres	Uneshiroreishigaidamashi		3.0±1.9	3.0±1.9				2.0±2.0	1.0±1.0		
Morula granulata	Reishigaidamashi								2.0±2.0		
Thais pseudodiadema	Ohaguroreishigai										
Thais squamosa	Koiwanishi								1.0±1.0		
Japeuthria cingulata	Shimabekkoubai										
Nassarius coronatus	Iboyoubai										1.0±1.0
Nassarius semisulcatus	Atsumushirogai	1.0±1.0	3.0±1.0	2.0±1.2	1.0±1.0			4.0±1.6	5.0±1.9	2.0±2.0	
Nassarius velatum	Shiinomiyoubai									1.0±1.0	
Pusiostoma mendricaria	Noshigai							1.0±1.0			
Pterygia dactylus	Imohude	1.0±1.0						1.0±1.0			
Vexillum balteolatum	Minomushigai			1.0±1.0	1.0±1.0					1.0±1.0	
Vexillum grueneri	Haiirominomushigai										
Vexillum michaui	Konntsukushigai					1.0±1.0					
Vexillum rugosum	Shiwaminomushigai			1.0±1.0							5.0±5.0
Clavus unizonaris	Hitosujitsunokudamaki										
Conus cornatus	Juzukakesayagataimogai										1.0±1.0
Conus ebraeus	Madaraimogai										
Onchidium verruculatum	Isoawamochi										
Siphonariidae laciniosa	Koudakakaramatsugai							4.0+4.0	16.0±9.1	8.0±5.7	
Barbatia amygdalumtortum	Beniegai										
Barbatia cruciata	Kurominoegai									1.0±1.0	
Barbatia virescens	Kariganeegai							1.0±1.0			
Striarca symmetrica	Mimiegai									2.0±1.2	
Modiolus auriculatus	Ryukyuhibarigai										
Pinctada maculata	Midoriaorigai									1.0±1.0	
Isognomon pernum	Kaishiaorigai				1.0±1.0				3.0±3.0	20.0±20.0	
Chama iostoma	Kanetsukezarugai		1.0±1.0			3.0±1.9			1.0±1.0		
Cardita leana	Tomayagai										
Leucosia perlata	Hutamekobushigani										
Oreophorus latusoides	Tsunokaruishikobushi										
Philyura taekoae	Amamimamekobushigani										
Micippa philyra	Kowatakuzugani				1.0+1.0						
Parthenope calappoides	Abatahishigani								1.0±1.0		
Kraussia rugulosa	Shiwagoishigani								1.0±1.0		
Kraussia truncatifrons	Hutabagoishigani			1.0±1.0							
Portunus bidens	Sagamihimegazami										1.0±1.0
Thalamita prymma	Benitsukegani										
Actumnus setifer	Suehiroibotegani										
Pilumnus uespertilio	Kebukagani				1.0±1.0						
Nanosesarma gordoni	Himebennkeigani										
Pachygrapsus mimutus	Himeiwagani										
Pseudograpsus elongatus	Kounagaiwaganimodoki										
Macrophthalmus serenei	Menagaosagani										
Macrophthalmus bosci	Himekakuosagani										
Uca perplexa	Okinawahakusennshiomaneki							1.0±1.0			
Uca tetragonon	Rurimadarashiomaneki										
Ophiocoma dentata	Gomahukumohitode							1.0±1.0	4.0±2.3		
Ophiarachnella infernalis	Minamiitsutsumekumohitode										
Holothuria leucospilota	Nisekuronamako								2.0±2.0		
Anadara antiquata	Ryukyusarubougai										1.0±1.0
Anodontia edentula	Kaburatsukigai										
Pillucina pisidium	Umenohanagai										
Pseudegaleomma rosea	Barairomameagemakigai										
Atactodea striata	Isohamaguri						6.0±2.6				
Coecella chinensis	Kuchibagai										
Exotica transculpta	Hasumezakuragai			1.0+1.0							
Loxoglypta compta	Mikunishiborizakuragai										
Pinguitellina pinguis	Migakihimezaraga										
Quadrans gargadia	Ootogeunegai										
Semelangulus tokubei	Komezakura										
Tellina staurella	Himenikkougai										
Asaphis violascens	Ryukyumasuogai	47.0±16.1	2.0+2.0				42.0±17.9	1.0±1.0			
Semele carnicolor	Samezaragaimodoki			3.0±1.9					2.0±1.2	1.0±1.0	
Donax faba	Ryukyunaminokogai	1.0±1.0					1.0±1.0				
Gafrarium pectinatum	Hososujinamigai			1.0±1.0	1.0±1.0					1.0±1.0	
Gafrarium tumidum	Arasujikemann		6.0±3.5	3.0±1.9				3.0±1.9	4.0±1.6		
Irus mitis	Matsukaze										
Pitar citrinum	Yuukagehamaguri										
Ruditapes variegatus	Himeasari	1.0±1.0	26.0±9.3				2.0±1.2	11.0±3.8			
Tapes literatus	Ryukyuasari										

(C) Shore C (continued)

Species	Mar 1998					Jun 1998					Sep 1998				
	0.90m	0.56m	0.43m	0.31m	0.23m	0.90m	0.56m	0.43m	0.31m	0.23m	0.90m	0.56m	0.43m	0.31m	0.23m
P. striata	7.0±4.1	17.0±1.0	1.0±1.0				5.0±1.0					2.0±1.2			
P. pygmaea		27.0±14.1					5.0±1.9					4.0±1.6			
E. variegta			1.0±1.0						1.0±1.0				3.0±3.0		
N. albicilla			4.0±1.6				2.0±1.2	8.0±2.8				1.0±1.0	7.0±5.7		
N. polita															
N. bensoni															
N. squamulata	3.0±1.9	26.0±9.3	10.0±3.5			2.0±1.2	7.0±3.0	9.0±6.6	2.0±2.0		4.0±1.6	24.0±2.3	11.0±4.1		
M. labio	23.0±12.9	15.0±10.4				17.0±17.0	18.0±9.3	1.0±1.0				5.0±2.5			
T. maculatus															
L. peroni								1.0±1.0							
C. costulosa			1.0±1.0					1.0±1.0							
L. granulata	10.0±8.7	49.0±18.4	1.0±1.0			2.0±2.0	13.0±3.0	3.0±1.0				17.0±3.4			
S. phymotis													1.0±1.0		
T. granifera															1.0±1.0
C. batillariaeformis		101.0±15.0	457.0±227.2	1.0±1.0			145.0±50.0	207.0±15.6	6.0±6.0			138.0±55.0	433.0±133.4	2.0±2.0	2.0±1.2
C. bifasciata						13.8±6.4	0.8±0.8				4.5±1.8	0.5±0.5			
C. irrorata															
C. subbrevicula							4.0±2.8					28.0±16.6			
P. acutangulus															
P. parcus					1.0±1.0										
R. vertagus								1.0±1.0							
P. sulcatus	5.0±5.0														
S. urceus										2.0±2.0					
C. annulus				1.0±1.0	2.0±2.0									2.0±2.0	
C. errones														1.0±1.0	
C. moneta															
N. fasciata															4.0±2.3
N. gualtieriana			1.0±1.0					2.0±1.2				1.0±1.0			
P. pyriformis															1.0±1.0
C. nicobaricum															
M. fusca	1.0±1.0	2.0±2.0										4.0±1.6			
C. fiscella				1.0±1.0										1.0±1.0	
C. margariticola		5.0±1.9	17.0±2.5	12.0±2.8			1.0±1.0	14.0±5.8	24.0±2.8	1.0±1.0			13.0±3.0	6.0±3.5	
M. anaxeres			3.0±1.9				1.0±1.0	4.0±2.8					2.0±2.0		
M. granulata			1.0±1.0					1.0±1.0							
T. pseudodiadema								1.0±1.0							
T. squamosa															
J. cingulata		1.0±1.0													
N. coronatus															1.0±1.0
N. semisulcatus			2.0±2.0				4.0±2.8					6.0±2.0	2.0±2.0		
N. velatum															
P. mendicaria															
P. dactylus	1.0±1.0														
V. balteolatum															
V. grueneri															1.0±1.0
V. michaui															
V. rugosum			1.0±1.0		1.0±1.0		3.0±1.9			1.0±1.0					
C. unizonaris															
C. cornatus															
C. ebraeus		1.0±1.0					1.0±1.0								
O. verruculatum				1.0±1.0										1.0±1.0	
S. laciniosa															
B. amygdalumtortum				3.0±1.9											
B. cruciata															
B. virescens						2.0±2.0		1.0±1.0	3.0±1.9					1.0±1.0	
S. symmetrica			1.0±1.0												
M. auriculatus				1.0±1.0					2.0±1.2				1.0±1.0		
P. maculata															
I. pernum		1.0±1.0		7.0±7.0					22.0±13.7						
C. iostoma			2.0±1.2	3.0±3.0				1.0±1.0	1.0±1.0				2.0±1.2	1.0±1.0	1.0±1.0
C. leana									1.0±1.0						
L. perlata															
O. latusoides				1.0±1.0									1.0±1.0		
P. taekoae					3.0±1.9										
M. philyra															
P. calappoides															
K. rugulosa			1.0±1.0	2.0±1.2				2.0±1.2	1.0±1.0					1.0±1.0	
K. truncatifrons															
P. bidens															
T. prymna					1.0±1.0					2.0±1.2				1.0±1.0	
A. setifer				6.0±3.5					1.0±1.0						
P. uespertilio								1.0±1.0	1.0±1.0						
N. gordoni													1.0±1.0		
P. mimutus									1.0±1.0						
P. elongatus	1.0±1.0					2.0±2.0									
M. verreauxi							1.0±1.0		1.0±1.0	19.0±8.7					2.0±2.0
M. bosci				5.0±2.5										1.0±1.0	
U. perplexa		1.0±1.0													
U. tetragonon												1.0±1.0			
O. dentata								8.0±3.3							
O. infernalis			10.0±1.2												
H. leucospilota															
A. antiquata															
A. edentula					1.0±1.0										
P. pisidium			3.0±3.0							2.0±1.2					
P. rosea										1.0±1.0					
A. striata	3.0±3.0					16.0±7.1					9.0±5.7				
C. chinensis											2.0±2.0				
E. transculpta					7.0±1.9					2.0±1.2				2.0±1.2	4.0±2.8
L. compta															0.3±0.3
P. pinguis					1.0±1.0					1.0±1.0					
Q. gargadia															
S. tokubei										0.3±0.3					
T. staurella				2.0±1.2	1.0±1.0					1.0±1.0				3.0±1.9	1.0±1.0
A. violascens	43.0±11.0					50.0±2.0					21.0±6.6				
S. carnicolor			4.0±2.3	1.0±1.0				2.0±1.2					2.0±2.0	1.0±1.0	
D. faba															
G. pectinatum			1.0±1.0	1.0±1.0				2.0±1.2	1.0±1.0				4.0±4.0	4.0±1.6	
G. tumidum		4.0±1.6	3.0±1.9	1.0±1.0			2.0±2.0					4.0±2.8	2.0±1.2		
I. mitis									1.0±1.0						
P. citrinum															3.0±1.0
R. variegatus	1.0±1.0	16.0±4.9					14.0±7.4				4.0±1.6	17.0±6.4			
T. literatus				1.0±1.0											

ACKNOWLEDGEMENTS

We appreciate the comments of Dr. R. Sato and reviewers on the manuscript. We acknowledge the information of Dr. A. Iijima about boulder shore fauna. We thank the staff of Ishigaki Tropical Station for their assistance in sampling and data input. This study was partly supported by funds from a grant of Seikai Nat. Fish. Res. Inst. Project.

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日本亜熱帯域の石垣島の転石海岸潮間帯における表在性動物と内在性動物の種組成

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小林　正裕・加藤　雅也・水戸　啓一

抄　　録

日本亜熱帯域に位置する石垣島の転石海岸において，潮間帯性の表在性動物と内在性動物の種組成を定量的に調査した．各生物を4～5季節×3つの浜×5～6潮位においてコドラートで採集した．総計112種の表在性動物と27種の内在性動物を採集した．表在性動物では，移動性動物（97種）が固着性動物（15種）より高い種数を示した．この移動性動物の中では，腹足類が最多種数を占め（68種），うちマルアマオブネ *Nerita squamulata* が高密度分布していた（各浜における最高密度：50.0～500.0m^{-2}）．一方，固着性動物では，二枚貝類が最多種数を占めた（14種）．内在性動物では，二枚貝類が最多種数を占め（26種），リュウキュウマスオガイ *Asaphis violascens*（各浜における最高密度：12.0～83.0m^{-2}）とヒメアサリ *Ruditapes variegatus*（5.6～26.0m^{-2}）が高密度分布し，10種類もの食用貝類が存在していた．以上の種の組成において，1）浜による変化は内在性動物より表在性動物において顕著で；2）季節間変化は内在性動物・表在性動物ともに幾つかの浜で激しく；3）潮位間変化は内在性動物・表在性動物ともに著しかった．これらの種組成変化や，固着性動物の乏しさについて，転石海岸固有の環境要因の影響を議論した．

琉球列島近海のカドミウムとリン酸塩の関係

阿　部　和　雄

Relationship between Cd and PO_4 off the Ryukyu Islands.

Kazuo Abe*

ABSTRACT

Relationship between Cd and PO_4 off the Ryukyu Islands was investigated. Water samples were collected using acid-cleaned Niskin bottles attached to CTD-RMS system, aboard R/V "Yoko-Maru" of Seikai National Fisheries Research Institute in May 1998. Preformed Cd and PO_4 were estimated from the equations as follows:

$Cd(P) = Cd(m) - AOU \cdot a/138$, $PO_4(P) = PO_4(m) - AOU/138$

where Cd(P) and PO_4(P) are preformed Cd and PO_4, Cd(m) and PO_4(m) are measured (observed) ones, respectively. AOU represents apparent oxygen utilization and "a" denotes the ratio of the regenerated Cd to PO_4 (nM/μM). Cd vs. AOU plot indicated the slope of 0.00105 (nM/μM) and 0.145 (nM/μM) as "a" above 400 m. Preformed Cd and PO_4 were nearly zero in surface layer and increased with depth below 400 m, and reached approximately 0.7 nM and 1.2 μM, respectively in deep water (below 1,000 m). The relationship between Cd and PO_4 showed a clear deviation. Above 400 m, the slope of the regression line was 0.131 ($nM_{Cd}/\mu M_{phosphate}$), and this value was much the same as the regeneration ratio of Cd to PO_4, which suggested that regeneration process might be a main factor that regulated the correlation of Cd and PO_4 in this layer. Below 400 m, the Cd/PO_4 ratios increased gradually with depth to the almost constant value of 0.36 (nM/μM) below 1,000 m, which is considered to be attributable to the apparent conservative mixing between water masses with originally different Cd/PO_4 ratio (different preformed values), in deep and shallow layer.

平成12年1月26日受理（Received January 26, 2000）
西海区水産研究所業績600号（Contribution from Seikai Fisheries Research Institute, No. 600）
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は じ め に

海洋におけるカドミウムは，一次生産活動と深く結びついた元素として知られており，生物生産に何らかの影響を与える物質と考えられている．その鉛直分布は一般に，外洋域においては栄養塩型の分布を示し，表層付近では植物プランクトン等の生物による取り込みのために枯渇し，深度増加に伴って有機物の分解・再生に起因する濃度増加を示し，水深1,000m付近に濃度のピークが認められる．カドミウムは栄養塩の中でも特にリン酸塩や硝酸塩との相関性が高く，外洋域における二成分の関係は直線関係で示される場合が多い（例えば Bruland et al., 1978: Bruland, 1980; Knauer and Martin, 1981; Matsunaga and Abe, 1985)．しかしながら海域によっては必ずしも直線関係ではなく，折れ曲がった直線として示され，これらの関係は生物生産活動を含めた海域特性を深く反映しているものと考えられる．これら二成分の関係は生物化学的循環，海水の物理的混合，堆積物や大気からの供給等多くの要因により支配されるものと考えられる．一方，栄養塩等の生物生産関連物質は，海域においては見かけ上その全てが生物生産に利用されるわけではなく，利用されない区分は保存性区分として非保存性区分と区別され，リン酸塩では保存性区分による水塊特性も論じられてきた．本報告では，琉球列島近海の北太平洋亜熱帯海域の観測点においてリン酸塩及びカドミウムの保存性区分を求め，両成分の相互関係について考察した．

方 法

石垣島近海の北太平洋の観測点，Stn. 1（22°30′N, 123°40′E）において1998年５月に，西海区水産研究所「陽光丸」により酸洗いしたニスキン採水器を用いて鉛直的に採水を行った（Fig. 1)．得られた海水試料は調査船デッキ上で酸洗いしたポリエチレン瓶に移し，試料の汚染を防止するために二重にポリエチレン袋に

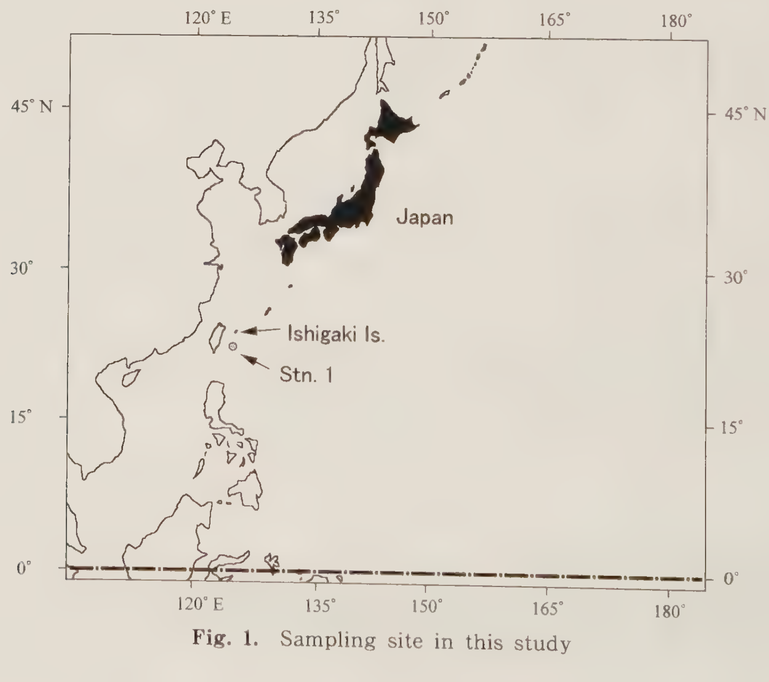


Fig. 1. Sampling site in this study

入れ，直ちに－40℃で凍結保存し，その後陸上の実験室内で解凍後分析を行った．溶存カドミウム分析は未濾過海水を Boyle & Edmond (1977) の APDC-Co 共沈法を若干改良して，無炎原子吸光分光光度法により定量を行った．分析法の概要は以下の通りである．海水試料100mlに超高純度塩酸を添加し pH を2に調整後，塩化コバルト，APDC 溶液を順次添加，撹拌後5分間静置し沈殿を熟成させる．この沈殿を 0.6μm ヌクレポアーフィルター上に集めて濾紙ごとテフロン製密閉容器へ入れ，濃硝酸を加え，70℃で1時間沈殿を高温・高圧で溶解させる．室温に戻した後に超純水（ミリ Q）で希釈し，無炎原子吸光分光光度計（日立 Z-8270）で定量した．なお，実験室内における操作はクラス100クリーンドラフト内で行い，溶存カドミウムの分析精度は 76pM で±2.4%，またブランク値は 1.7pM である．

リン酸塩の分析は凍結試料を解凍後に比色法，溶存酸素は船上でウインクラー法により定量した．また現場の塩分・水温は CTD により観測を行った．

結 果 と 考 察

1)　海況及び鉛直分布

Fig. 2 に Stn. 1 における塩分・水温図を示した．この海域は亜熱帯海域に属し，水深250m付近の亜表層に水温約20℃，塩分約34.9の塩分極大と水深600m付近に水温約9℃，塩分34.3以下の塩分極小層が存在し，北太平洋亜熱帯海域の特性を表している．本調査海域近海における海域特性の詳細に関しては他の文献等を参照されたい（例えば Takahasi and Chaen, 1967；1969；1971；宮地ら，1994）．

Stn. 1 におけるカドミウムとリン酸塩の鉛直分布を Fig. 3 に示した．水深2,000mまでの分布を示しているが，両成分ともに表層付近で枯渇し，深度増加に伴ってその濃度の増加が観測され，1,000m付近でほぼ一定の値に達し，リン酸塩で 2.8μM，カドミウムは 0.9nM 程度の値を示している．これらの分布は表層付近で主に植物プランクトンにより取り込まれたものが，水柱内を沈降する過程で分解・再生された結果であると考えられ，多くの海域，特に外洋域において同様の分布パターンが報告されている．

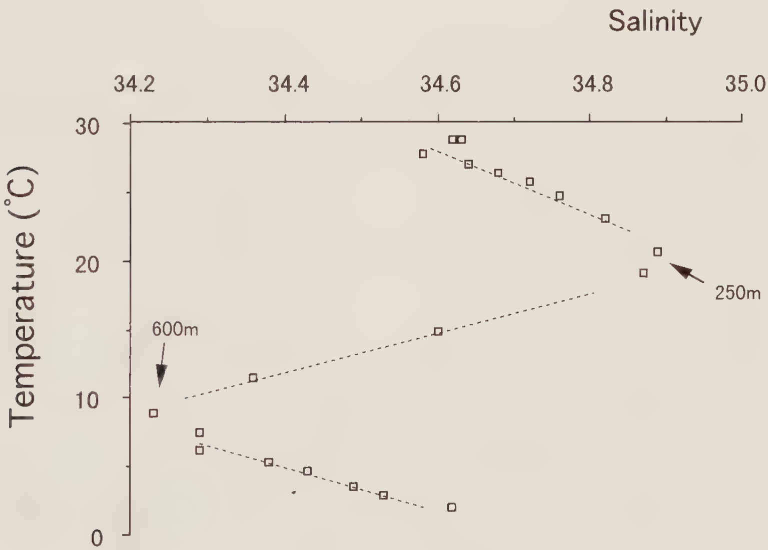


Fig. 2. T–S diagram off the Ryukyu Islands. Data at 250 m and 600 m are indicated in this figure.

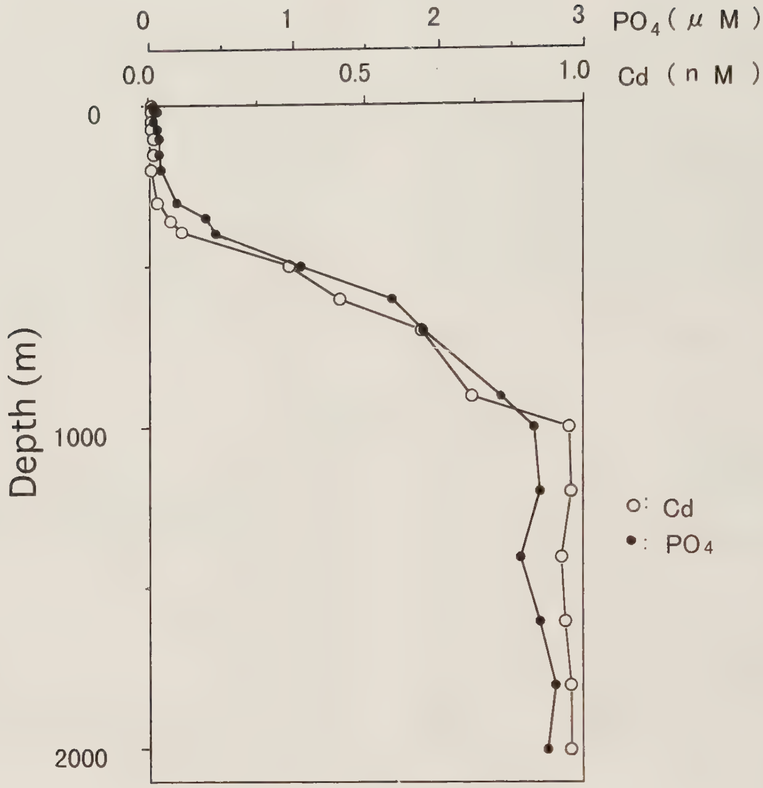


Fig. 3. Vertical distributions of Cd and PO_4.

2) カドミウム，リン酸塩と AOU（見かけの酸素消費量）の関係

表層付近で生産された有機物（植物プランクトン）は水柱内で酸化分解を受け海水中へと再生される．この際海水中に溶けている溶存酸素を使用し，海水中では溶存酸素の減少として記録される．溶存酸素量は水温・塩分により飽和度が異なることから，その増減には飽和度から観測値を差し引いた AOU（見かけの酸素消費量）を用いる必要がある．平均的な植物プランクトンの生産，分解・再生過程を表す式としてレッドフィールドの式（Redfield, et al., 1963）が提唱されたが，Kudo et al. (1996) は南太平洋でのカドミウム（Cd）の観測結果をこの式に組み込んで分解・再生モデルによる分布特性の説明を試みた．用いた式は以下の通りである．

$$(CH_2O)106(NH_3)16H_3PO_4Cda + 138O_2 = 106CO_2 + 16HNO_3 + H_3PO_4 + 122H_2O + aCd \quad (1)$$

左辺が生物生産，右辺が分解・再生を表している．ここでリン酸塩 1 モルの再生に対して酸素（分子）は 138モル消費されることを意味しているが，同様にカドミウム a モルに対して酸素（分子）は138モル，つまりカドミウム 1 モルに対して 138/a モルの酸素（分子）が消費されることになる．この際再生されるリン酸塩とカドミウムのモル比はモデル中の平均的な有機物中のカドミウムのモル比，つまり“a”ということになる．

リン酸塩及びカドミウムの観測値と AOU の関係を Fig. 4 に示した．Fig. 4-a はリン酸塩との関係であるが，図中の直線はレッドフィールドの式で表される再生比の 1：138 に相当し，傾きは7.2×10^{-3}

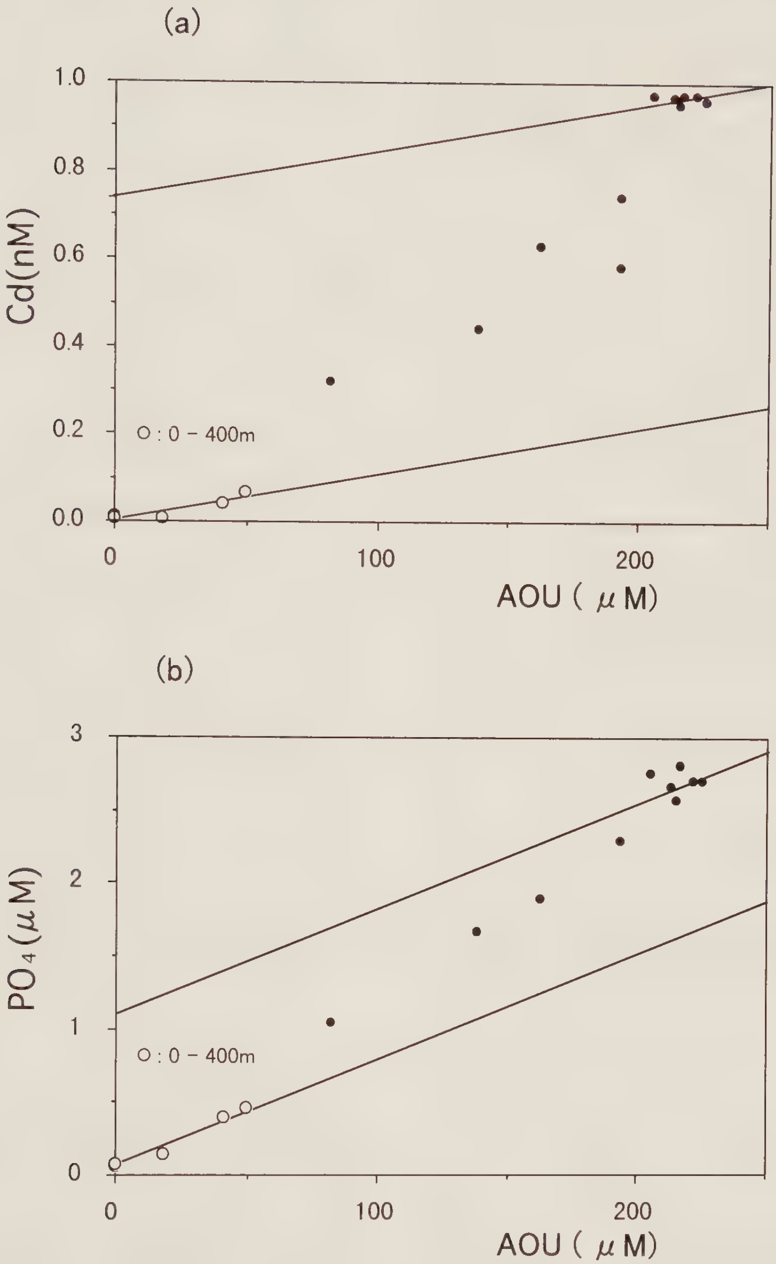


Fig. 4. Relationship between AOU and Cd(a), PO_4(b). In Fig. 4–b, the straight line shows the regeneration ratio to AOU for PO_4 of "1 : 138" in "Redfield's equation".

($\mu M_{phosphate}/\mu M_{AOU}$) である．ここに示されるように水深400mまでのリン酸塩の値はこの直線の周りにばらつき，本研究海域ではリン酸塩に関して古典的な再生比が適応できるものと考えられる．また，AOU がゼロの時のリン酸塩の値は有機物（植物プランクトン）の生産，分解・再生に無関係な保存性区分を表すが，以下の式により求めることができる．

$$PO_4(P) = PO_4(O) - AOU/138 \qquad (2)$$

$PO_4(P)$, $PO_4(O)$ はそれぞれ保存性区分及び実測値のリン酸塩濃度である．保存性リン酸塩は Fig. 4(b) 中に縦軸切片として表されているが，リン酸塩と AOU の分解・再生比が深度により変動しないと仮定すると，保存性区分は AOU の増加，つまり深度増加に伴って値が大きくなる傾向が認められる．保存性リン酸塩は1,000m以深でほぼ一定の値となり，その平均値は 1.18nM であり，この値は太平洋深層水の値（Kudo, et al., 1996）とほぼ一致する．

保存性リン酸塩の分布より水深400mまではほぼ同様の性質を有する水であると判断し，カドミウムに関してはこの深度までの以下の回帰直線を求め，再生比を求めた．

$$Cd = 0.00573 + (0.0105 \times 10^{-3}) \times AOU (r = 0.952) \qquad (3)$$

(3)式における直線の傾きは0.00105×10^{3} ($nM_{Cd}/\mu M_{AOU}$) であり，分解・再生時に消費される溶存酸素と再生されるカドミウムのモル比は 1：949,000 となる．さらに，この際分解・再生されるリン酸塩との比はこの直線の傾きをリン酸塩と AOU の関係式の傾き (7.2×10^{-3}) で除して0.145 ($nM_{Cd}/\mu M_{phosphate}$) の関係が得られた．また，保存性カドミウムは次式により定義できる．

$$Cd(P) = Cd(m) - AOU \cdot a/138 \qquad (4)$$

Cd(P), Cd(m) は保存性及び実測のカドミウム濃度，"a" は分解・再生される時のカドミウム/リン酸塩比であり，表層水中で植物プランクトンに取り込まれた時の比を示している．リン酸塩と同様に分解・再生時における AOU との比が深度により一定であると仮定すると，保存性カドミウムも AOU の増加，つまり深度とともに増加し1,000m以深でほぼ一定の値に達し，平均値で0.740を示した (Fig. 4–a)．分解・再生される非保存性区分は実測値から保存性区分を差し引いて求めることができるが，1000m 以深ではこの区分はカドミウム，リン酸塩でそれぞれ23.5，56.6%となりこれらは北太平洋深層水中の値とほぼ等しい結果となった（Kudo et al., 1996）．

3) リン酸塩とカドミウムの関係

リン酸塩とカドミウムの関係を Fig. 5 に示した．図中の直線は水深400mを境として二本の回帰直線を求めたものであるが，水深400m以浅では以下のような関係になった．

$$Cd = -0.00142 + (0.131 \times 10^{-3}) \times PO_4 (r = 0.988) \qquad (5)$$

(5)式では直線の傾きは0.131 ($nM_{Cd}/\mu M_{phosphate}$) であり，ほぼ原点を通る直線関係が示された．この傾きは北太平洋で一般に報告された値（Bruland, et al., 1978；Bruland, 1980；Knauer and Martin, 1981；Bruland 1994）よりも小さく（約 1/3），極域を除く南太平洋の値（Frew and Hunter, 1995；Kudo et al., 1996）よりも僅かに大きな値であり，本調査海域における西部北太平洋亜熱帯海域の特性を表しているものと考えられる．また，この傾きは本研究で求めた分解・再生時におけるカドミウム/リン酸塩比 (0.145) と非常に近似した値であり，本海域における表層付近の両成分の関係は主に有機物（植物プランクトン）の分解・再生が大きく影響しているものと考えられる．水深400m以深における回帰直線は以下の通りである．

$$Cd = -0.187 + (0.416 \times 10^{-3}) \times PO_4 (r = 0.954) \qquad (6)$$

このように回帰直線は比較的大きな傾き (0.416, $nM_{Cd}/\mu M_{phosphate}$) 及び明瞭な負の切片を持つ直線として示されているが，これは400m付近および1,000m以深の二つの水塊が希釈混合した結果であると考えられる．それぞれの深度（現場）におけるカドミウム/リン酸塩比はリン酸塩の増加，つまり深度増加に伴って次第に大きくなり，1,000m付近よりほぼ一定の値（平均，0.357）となる．この値は太平洋深層水が固有に持っている値（De Baar et al., 1994）とほぼ同程度であり，この深度増加に伴うカドミウム/リン酸塩比の

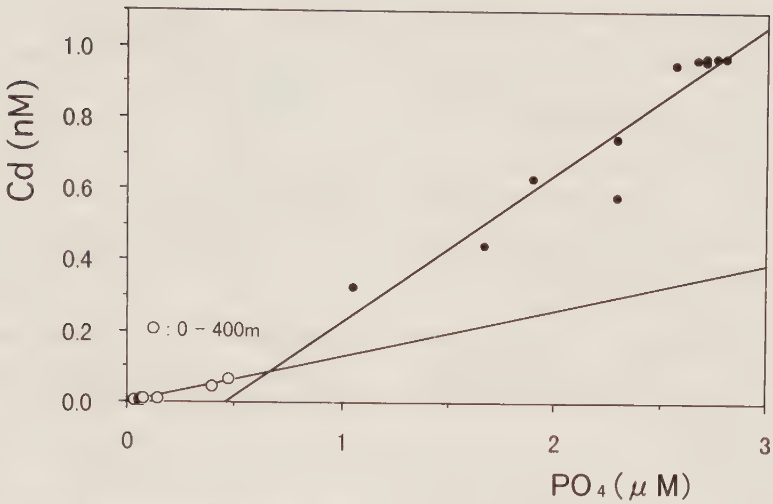


Fig. 5. Relationship between Cd and PO_4 off the Ryukyu Islands.

増加は保存性区分の変動に起因するものと考えられる．つまり400m付近ではカドミウム/リン酸塩比は表層における比，0.131に近いものであるが，この比を持つ水塊と1,000m以深の0.357を比に持つ二つの水塊との希釈混合により，400m以深のカドミウムとリン酸塩の直線関係が保たれているものと考えられる．

以上述べたように，琉球列島近海の亜熱帯海域におけるカドミウムとリン酸塩の関係は表層付近及びそれ以深の二本の直線関係として示される（Fig. 5)．表層付近で求められた直線の傾きは，植物プランクトンの分解時において再生されるカドミウム/リン酸塩比と似通っていることから，分解・再生及び生物による取り込みがこれらの相互関係を支配する大きな要因であると考えられる．また水深が400mよりも深いところでは，異なったカドミウム/リン酸塩比を持つ水塊が希釈混合した結果，二成分の間に直線関係が保たれているものと考えられる．

謝　辞

本研究を行うに当たり試料採取に際し，西海区水産研究所「陽光丸」船長以下乗組員の方々及び西海区水産研究所海洋環境研究室岡慎一郎主任研究官のご協力に感謝します．

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長崎県野母崎において1998年秋に発生したクロメ葉状部欠損現象の経過観察

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Recovery of *Ecklonia kurome* after the Occurrence of Blade Disappearing Phenomenon at Nomozaki, Nagasaki Prefecture

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ABSTRACT

In autumn of 1998, the blade disappearring phenomenon assumed to be results of grazing by herbivorous fishes was observed on *Ecklonia kurome* along the shallow coastal waters at Nomozaki. We investigated the recovery of *E. kurome* after the autumn event at Ôtategami–iwa and Kotategami–iwa in Nomozaki area until the following spring. At Ôtategami–iwa, the thalli having regenerated blades were observed in shallower than 2 m depth, but did not in deeper than 3 m depth. At Kotategami–iwa, 2 km distant from the Ôtategami–iwa, the thalli having regenerated blades were recognized in all the depth from 0 to 13 m, and dense *E. kurome* beds as well. From the existence of arc–shape scars on the newly growing blades collected at the two sites on March 1999, the grazing by herbivorous fishes was thought to have continued during the following winter. The differences in degree of recovery between the two sites and among different water depths may be resulted from the continuity and intensity of the grazing by fishes. During these investigations, we also found remarkable undergrowth of *Sargassum hemiphyllum* and *Hizikia fusiformis* having no apical growth point in the shallow waters. These

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平成12年３月９日　受理（Received March 9, 2000）
西海区水産研究所業績第604号（Contribution from Seikai National Fisheries Research Institute, No. 604）
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phenomena were presumed to be caused by the grazing of herbivorous fishes, different from those consumed *E. kurome*.

は　じ　め　に

長崎県野母崎において，1998年９月に葉状部が著しく欠損したクロメ *Ecklonia kurome* が観察された（吉村・清本，1998）．同年11月から翌年１月にかけて長崎県下で行われた調査の結果，葉状部欠損の程度は水深や場所によって異なること，また，アラメ *Eisenia bicyclis*・カジメ *Ecklonia cava* を含めたコンブ科３種で同様の現象が県下で広く発生していることが確認された（桐山ら，1999）．残された葉状部の縁辺には弧状の痕跡が見られること，これらの一部が飼育下のブダイ *Calotomus japonica* によりつけられた採食痕に酷似することから，藻食性魚類の採食が原因である可能性が推測されている（桐山ら，1999）．本現象は1994年10月に近隣の三和町地先にて小規模な発生を見たことがある（吉村，未発表）が，このように広範囲に発生したのは初めてであり，今後の推移が懸念される．

そこで，筆者らは野母崎の当該水域において，本現象発生後の経過とクロメ葉状部の再生状況を潜水により調査した．この結果，本現象の発生が少なくとも1999年３月まで継続したこと，冬季の葉状部の再生状況が水深・調査地点によって大きく異なっていたこと等が明らかとなるとともに，イソモク *Sargassum hemiphyllum* やヒジキ *Hizikia fusiformis* でも主枝が著しく短くなっている個体が観察され，クロメ同様に藻食性魚類の採食によるものと推察されたのでこれらの概要を報告する．本文にはいるに先立ち，調査にご協力いただいた野母崎三和漁業協同組合に謝意を表する．

方　　法

２種類の調査を長崎県野母崎（Fig. 1）において，１回目1998年10月22日，２回目12月７日，３回目翌年３月25日の計３回，SCUBA 潜水によって実施した．第一の調査では大立神岩周辺（以下，大立）の同一転石上，第二の調査では地先一帯におけるクロメ葉状部の状態の推移を観察した．

第一の調査は大立の水深5.2ｍにおいて，クロメが優占する長径およそ１ｍの転石３個を選び，それらの上に生育する全てのクロメを対象に，茎長・中央葉長・最大側葉長を計測した．また，葉状部の状態を，側葉が３枚以上残る，側葉が３枚未満，側葉が無く中央葉の一部が残る，中央葉もなく茎と付着器のみ，の４段階で評価した．

第二の調査は，１回目は大立を，２回目は大立から小立神岩（以下，小立）に至る水域を，３回目は大立と小立の両水域を対象とした．１回目と２回目の調査では，全体的なクロメの生育状況を記録した．３回目は場所や水深による葉状部の再生状態の違いを明らかにするため，標本採取も行った．標本は，大立の水深１～２ｍ，３～４ｍ，４～５ｍのそれぞれで成体11～14個体の合計39個体，小立の水深８ｍで幼体32個体，成体25個体を採取した．また，最初の調査から藻食性魚類の関与が考えられたため，潜水調査中に観察された藻食性魚類を種毎に計数した．大立では，顕著に全長の短いイソモクとヒジキが観察されたため，これらも約40個体ずつ採取した．

採取したクロメについては，石田・由木（1996）に基づく年齢査定と全長・中央葉長・最大側葉長の測定を行った．また，同一年齢の健全な個体との比較によって，側葉の面積が1/2以上か以下かを判定した．また，葉状部が欠損したクロメでは葉縁に弧状の痕跡が見られた（Plate 1a）．これらは，藻食性魚類の採食痕と考えられること（桐山ら，1999）から，以下では弧状の採食痕とする．弧状の採食痕は，側葉部でははっきりしなかったが，中央葉では明確であったので，中央葉において採食痕の有無を調べ，特に茎と中央葉の移行部から短い側葉の基部までが損傷すると側葉の新生と伸長に重大な影響があるため，移行部から

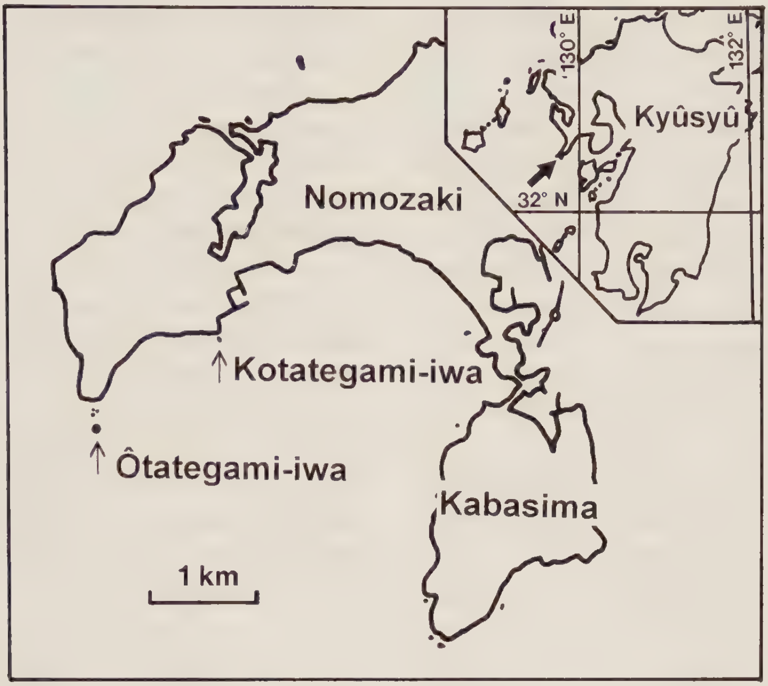


Fig. 1. Map of study sites.

5枚以内の新生葉（ここでは側葉長5㎝以下とする）までの範囲を「生長点付近」として中央葉の他の部分と区別した．この採食痕が見られたクロメの割合を，小立と大立とで比較するために，今回の測定結果に清本ら（2000）の小立における水深7ｍのクロメ2歳の結果も加えて，採集地・年齢間の多重比較を Steel–Dwass の方法（永田・吉田，1997）により行った．

ヒジキとイソモクについては，全長を測定し，葉における弧状の採食痕の有無を観察した．また，各株で長い方から3本までの主枝について，頂端部の生長点の有無を調べた．クロメ同様に，健全な個体との比較によって葉状部欠損状態の定量化を試みたが，健全な個体が調査海域に見られなかったため評価できなかった．

結　果

調査地の概況：大立は水深2ｍまでは急勾配で立ち上がる岩盤が多く存在しているが，2ｍ以深は比較的起伏の少ない岩盤・転石地帯が水深およそ15ｍまで続く．ウスバノコギリモク *S. serratifolium*，トゲモク *S. micracanthum* などのホンダワラ属が優占し，これらにクロメが混生する．

小立は水深12ｍまでは起伏の大きな岩盤が続き，12ｍ以深は平坦な砂地となる．クロメが優占し，ノコギリモク *S. macrocarpum*，ウスバノコギリモク，及び，エンドウモク *S. yendoi* が混生している．

転石上のクロメの推移：大立の3つの転石上では，10月22日には29個体のクロメ成体が存在した．葉状部の状態別に見ると，側葉を全く持たないものが12個体（41%），少なくとも1枚の側葉を有するものが17個体（59%）で，後者の中央葉長は平均14.9㎝，最大側葉長は平均24.9㎝であった（Table 1）．同年12月7日には側葉を有する個体は全く見られず，茎と付着器だけになったものが19個体（86%）と大半を占め，いずれも残された茎の先端部は腐敗していた．翌年3月25日には，すべての成体は茎が流失しほぼ付着器のみとなっ

ていたが，新たに計207個体の幼体（全長20～215mm）が高密度に入植していた．これらの幼体には弧状の採食痕は見られなかった．

地先一帯の推移：1回目の大立における調査では，クロメ成体は水深6m以浅に見られたが，5m以深では全てが葉状部のほとんどを失い茎と付着器のみで，水深が浅くなるにつれて中央葉や側葉のあるものが見られるようになり，2m以浅ではほぼ正常な個体の割合が高くなった．一方，幼体は水深7m以浅で見られたが，葉状部に欠損は見られなかった．これに対して，2回目の小立における調査では，クロメの成体・幼体ともに12m以浅で見られ，葉状部の欠損は2m以深の成体で多かった．

3回目の調査では，小立では全域で葉状部の再生が観察されたが，大立では再生が観察されたのは4m以浅で，3m以深では再生は不良であった．ただ，幼体は水深10m以浅の全ての水深において高密度に認められた（Plate 1h）．この時採集したクロメのうち，再生が良好なもの，再生しているものの異常なもの，再生しなかった個体の写真を Plate 1b～e に示す．この日の観察中に大立でアイゴ31個体（目視によるおおよその体長は15～30cm）が観察されたが，それ以外の藻食性魚類は観察されなかった．

採集個体の測定結果：大立では，水深1～2mで採集したクロメ14個体（2歳，平均全長43.9cm）の最大側葉長は平均25.9cm，中央葉長は平均26.0cmであり，側葉面積が健全な個体の1/2以下のものはなかった（Table 2）．弧状の採食痕は7割の10個体で中央葉に見られ，そのうち，5個体では生長点付近にも見られた（Table 3）．水深3～4mで採集したクロメ14個体（3歳，平均全長32.9cm）の最大側葉長は平均8.7cm，中央葉長は平均18.2cmであり，側葉面積はすべて健全個体の1/2以下であった（Table 2）．弧状の採食痕は全ての個体で中央葉に認められ，8割をこえる12本で

Table 1.　The change in state of *E. kurome* on three boulders in 5.2 m depth at Ôtategami-iwa

Age	State*	1998/10/22 No.	1998/10/22 %	Length (mean±SD cm) Stipe	Primary blade	Longest lateral blade	1998/12/7 No.	1998/12/7 %	1999/3/25 No.	1999/3/25 %
>1	-	4	14	10.8±6.3	0±0	0±0	19	86	0	0
	+	8	28	13.6±8.3	12.1±5.9	0±0	3	14	0	0
	++	10	34	15.5±5.5	14.6±3.2	25.3±9.6	0	0	0	0
	+++	7	24	15.7±4.9	15.4±4.8	24.4±5.2	0	0	0	0
0		0	0				0	0	207	100

*－: Stipe and holdfaste without blades, +: no lateral blades remained, ++: less than 3 lateral blades remained, +++: more than 2 lateral blades remained.

Table 2.　The size and the state of lateral blade of *E. kurome* sampled on March 25, 1999

Sample site	Depth (m)	Age	No.	Length (mean±SD cm) Total	Primary blade	Longest lateral blade	State of lateral blade (%)** >1/2	<1/2	No blade
Ôtategami-iwa	1–2	2	14	43.9±5.4	26.0±6.7	25.9±6.6	100	0	0
	3–4	3	14	32.9±8.1	18.2±6.5	8.7±4.7	0	100	0
	4–5	3	11	9.5±2.2	0.2±0.6	0.1±0.3	0	18	82
Kotategami-iwa	8	3	25	52.2±8.6	12.2±6.4	27.2±5.7	88	12	0
	7*	2	31	41.0±5.6	34.7±6.0	19.5±4.7	97	3	0

*Cited from Kiyomoto et al. (2000).

**The state of lateral blades were classified into three categories; >1/2: more than half of normal blade, <1/2: less than half of normal blade, no blade: no lateral blade remained.

生長点付近にも見られた．水深４～５ｍで採集したクロメ11個体（３歳，平均全長9.5cm）では，葉状部が欠損したものが多く，８割の９個体は茎と付着器のみ，他の２個体でも側葉長は１cm以下，中央葉長も２cm以下にすぎなかった（Table 2）．

一方，小立では，水深８ｍで採集したクロメ幼体32個体（平均全長12.1cm）には側葉はまだ形成されておらず，葉長は平均11.5cmで，葉面積が健全な個体の1/2以下であったのは３個体であった（Table 4）．弧状の採食痕が認められたのは２個体に過ぎず，うち１個体は葉面積が1/2以下であった．同所で採集した３歳のクロメ25個体（平均全長52.2cm）の最大側葉長は平均27.2cm，中央葉長は平均12.2cmであり，側葉面積が1/2以下のものは３個体であった（Table 2）．弧状の採食痕が９割をこえる23個体で中央葉に見られ，うち１個体では生長点付近にも見られた（Table 3）．採食痕が生長点付近にも見られた１個体と中央葉に見られた１個体では側葉面積が1/2以下であった．

水深・採集地間の比較：クロメの中央葉・生長点付近に採食痕が認められた割合を，大立の水深１～２ｍの２歳（以下，大立２歳），３～４ｍと４～５ｍの３歳を一緒にしたもの（大立３歳），小立８ｍの３歳（小立３歳），および小立７ｍの２歳（小立２歳）の４者間で比較した（Table 3）．生長点付近に関しては小立２歳と３歳の値は極めて低く，両者の間には有意差はなかった．この両者と比較すると大立２歳の値（$p<0.01$）と大立３歳の値（$p<0.001$）はともに有意に高く，また，大立２歳の値は大立３歳の値よりも有意（$p<0.05$）に低かった．中央葉に関しては大立３歳と小立３歳の間に有意差はなく，この両者と比較すると大立２歳の値は有意に低く（$p<0.05$），小立２歳は他の３者よりもさらに低い値であった（$p<0.001$）．

ホンダワラ類の観察結果：大立で見られたホンダワラ類のうち，イソモク（Plate 1f）とヒジキは，全ての株で全長が極端に短く，刈り揃えられたような状態であった．主枝の先端が物理的に切断され生長点の無いものが多かった．この切断面周辺に退色や腐敗は見られず，治癒したと思われる主枝も見られた（Plate 1g）．採集したヒジキ41株の平均全長は11.7cmであり，22株の葉に採食痕が見られ，観察対象とした主枝102

Table 3. The proportions of *E. kurome* having arc-shape scars on their primary blades

Sample Site	Age	Depth (m)	No.	% of individuals with scars: Near growth point*†	% of individuals with scars: Primary blade†
Ôtategami-iwa	2	1-2	14	36^b	71^b
	3	3-4/4-5	16	87^a	100^a
Kotategami-iwa	3	8	25	4^c	92^a
	2	7	31	0^c	23^c

*Five lateral blades from the transit part between stipe and blade.
†Values in column with different superscripts differ significantly ($p<0.05$) by Steel-Dwass method.

Table 4. The size of young *E. kurome* sampled from 8 m depth at Kotategami-iwa on March 25, 1999, and the proportions of having blade less than half of normal one and having arc-shape scars on their blades

No.	Total length (mean±SD cm) (Min.-Max.)	Blade length (mean±SD cm) (Min.-Max.)	Blade area*: No.	Blade area*: %	Exist of arc-shape scar: No.	Exist of arc-shape scar: %
32	12.1±6.6 (2-26)	11.5±6.3 (2-24)	3	9	2	6

*Blade area less than half of normal shape.

Table 5. The size of two Sargassaceous species sampled at Ôtategami-iwa, on March 25, 1999, and the proportions of individuals having arc-shape scars on their thalli and having main stems without apical growth point

Species	Individual No.	Total length (mean±SD cm) (Min.-Max.)	Arc-shape scars		Main stem No.	Growth point lost	
			No.	%		No.	%
H. fusiformis (ヒジキ)	41	11.7±4.0 (4-21)	22	54	102	47	46
S. hemiphyllum (イソモク)	45	11.1±2.8 (5-16)	38	84	nd	nd	

本のうち先端に生長点のないものが47本あった (Table 5). 採集したイソモク45株の平均全長は11.1 cmであり，38株の葉に採食痕が認められた (Table 5). しかし，優占種であるトゲモクとウスバノコギリモク，さらにはノコギリモクにはこのような極端に主枝の短いものは認められなかった.

考　　　察

大立における追跡調査では，水深5.2mの特定した転石上に生育するクロメは3月にはすべて付着器のみとなり，この水域全体でも水深4～5mでは再生が認められなかった．一方，水深3～4mでは側葉が短いものが残る程度であったが，1～2mでは採食痕はあるものの葉状部は健全に生長していた．大立からわずか2kmしか離れていない小立においては，水深1～12mに生育するクロメの葉状部は再生し，ほぼ通常の状態に回復していた．大立のクロメは水深が浅いほど葉状部が回復したのに対し，小立のクロメは生育範囲の全ての水深で葉状部が再生しており，両地点間で葉状部の回復状況が異なっていた.

野母崎における葉状部欠損現象の原因として，葉状部に残された弧状の痕跡から藻食性魚類による採食が考えられている（桐山ら，1999)．今回の調査で採集したクロメに見られた弧状の採食痕も，いわゆる「末枯れ」時に見られる葉状部先端の変色や腐敗が見られないこと，波浪による物理的な切断としては弧状の形が整っていること等から，魚種の特定はできないものの，藻食性魚類の採食によるものと判断された．葉状部の採食痕は，大立と小立の両方で認められたが，採食痕の見られる個体数の割合は両地点で異なっていた．特に，生長点付近の欠損率は2年目・3年目の個体とも，大立で高く，小立で低い値であった．小島・谷口（1994）による徳島県のクロメにおける側葉新生状況の調査結果から判断して，本報告で生長点付近とした部位における短い側葉は，冬季に新生したものと考えられる．従って，生長点付近に見られた採食痕は冬季以降に新生した側葉を藻食性魚類が採食した結果であり，1998年秋の葉状部欠損現象の確認以降も藻食性魚類による採食は継続していたと考えられる．1999年3月に大立と小立でのクロメ葉状部の回復状況に大きな差が見られたのは，両域でのクロメ生長点付近の欠損率が異なっていたことから，藻食性魚類のクロメに対する冬季の採食圧が両域で異なった結果であると推測された.

大立ではヒジキ・イソモクの主枝が10cm位の長さに刈り揃えられたようになっていたが，ウスバノコギリモク・トゲモク・ノコギリモクではこのような現象は見られなかった．これらのヒジキ・イソモクでは，主枝の先端に生長点が見られないこと，退色や末端の腐敗が見られないことから生理的な原因とは考え難い．さらに，詳細に観察すると葉や小枝の部分に採食痕らしいものが認められたが，葉や小枝が細いため，クロメに見られたような弧状の特徴は見出せなかった．さらに，ヒジキ，イソモク両者は潮間帯下部から漸深帯の最上部と，クロメでは異常が見られなかった場所に生育する種であり，この原因が仮に魚類の採食であるとしてもクロメを採食したものとは種を異にする可能性が高いと考えられた.

このように，葉状部欠損現象は複数種の魚類によって引き起こされている可能性がある．本現象の機構を解明するためには，実験的研究を含めて原因種の特定を行うとともに，それらの行動や資源量を明らかにすることが必要であり，この分野の研究の進展が望まれる．また，調査海域からわずか3km東の樺島では1998年秋にもクロメ葉状部が健全であり（桐山ら，1999），水塊や波浪などの違い（新井，1988；中山・新井，1999）によって現象の発生が大きく左右される可能性もあり，これらの海洋環境との関係においても検討する必要がある．

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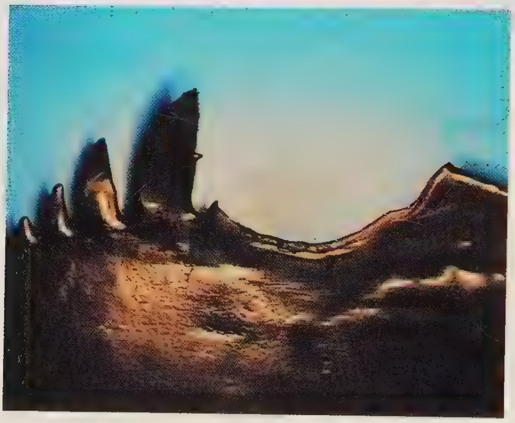
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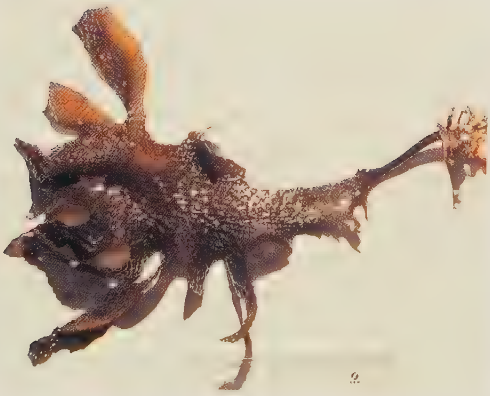
Plate 1. Photographs of algae observed at Nomozaki.



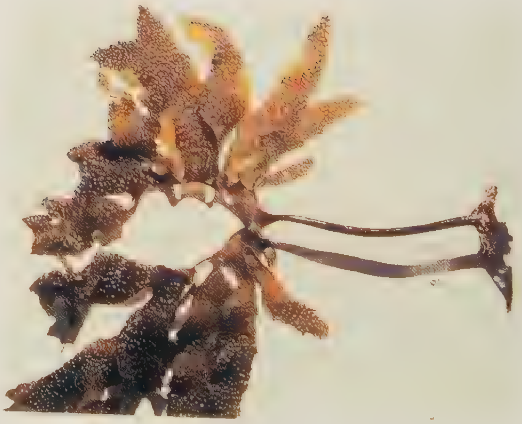
(a) Arc-shape scars on *E. kurome*.



(b) Well recovered *E. kurome*.



(c) Poorly recovered *E. kurome*.

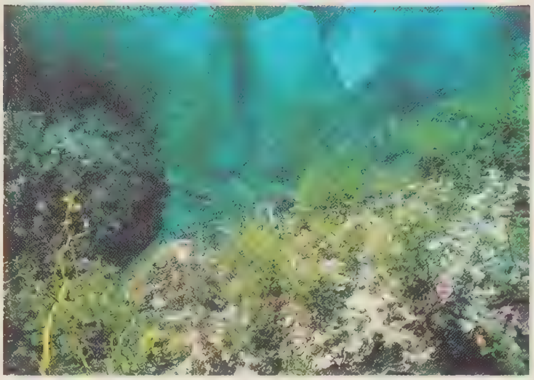


(d) Abnormally recovered *E. kurome*.

Plate 1. (cont.)



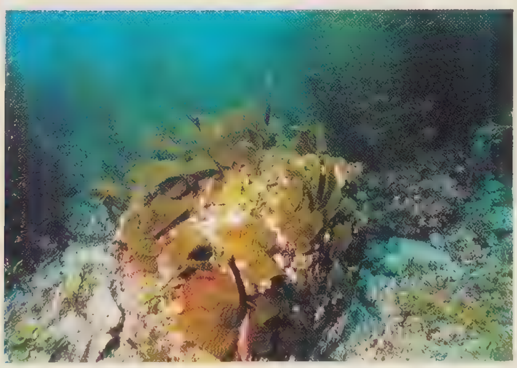
(e) Not recovered *E. kurome*.



(f) Undergrown *S. hemiphyllum* at sampled site.



(g) Tips of undergrown *H. fusiformis* with the section as if they are cut. New germination by vegetative reproduction occurred at the section (left).



(h) Dense patch of young *E. kurome*

長崎県野母崎の潮下帯に生育する大型褐藻5種に対する藻食性魚類の採食選択性

清本　節夫*・吉村　拓*・新井　章吾**

Grazing Selectivity of Herbivorous Fishes on Five Macroalgae in Sublittoral Zone at Nomozaki, Nagasaki Prefecture

Setuo Kiyomoto, Taku Yoshimura and Shogo Arai

ABSTRACT

Based on an assumption that grazing by herbivorous fishes is one of important factors responsible for the large scale disappearance of macroalgae blades, grazing selectivity of these fishes on large brown algae was studied in sublittoral zone at Nomozaki in Nagasaki Prefecture, Japan. Five species of brown algae, *Undaria pinnatifida, Ecklonia kurome, Sargassum macrocarpum, S. yendoi*, and *S. serratifolium*, were sampled on March in 1999 and arc-shape scars on each individual were investigated in detail.

The proportion of individuals having blades less than half of the normal blade area was 83% in *U. pinnatifida*, clearly higher than that of 0 to 3% in the other 4 species. Also, the proportion of individuals having arc-shape scars, thought to be the evidence of grazing, was 93% in *U. pinnatifida*, 23% in *E. kurome*, and less than 5% in the remaining 3 species. These results clearly indicate selective grazing by herbivorous fishes on *U. pinnatifida*.

The scars on the midrib of *U. pinnatifida* closely resembled the tooth marks artificially made by pressing the teeth of *Calatonus japonicus*, therefor *C. japonicus* is thought to be one of the grazers. More researches are needed to make clear participation of another fishes in grazing activity, and to elucidate the influences of fish grazing on the community structure of algae.

2000年3月21日　受理（received March 21, 2000）
西海区水産研究所業績第606号（contributions from Seikai National Fisheries Research Institute, No. 606）
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はじめに

1998年9月に長崎県野母崎においてクロメ *Ecklonia kurome* の葉状部が著しく欠損した個体が多数観察され，引き続いて行われた調査から長崎県下の各地でコンブ科海藻に同様な現象の発生が確認された（桐山ら, 1999). 筆者らが野母崎において引き続いて行った回復状況の調査で，この現象の出現頻度が大型褐藻の種によって大きく異なることに気がついた．そこで，コンブ目チガイソ科のワカメ *Undaria pinnatifida* とコンブ科のクロメ，および，ヒバマタ目ホンダワラ科のノコギリモク *Sargassum macrocarpum*，ウスバノコギリモク *S. serratifolium*，エンドウモク *S. yendoi* の大型褐藻5種が比較的均質に混生している岩盤において，標本を採取し，藻食性魚類の採食種選択性について検討を行った．また，歯形の比較から原因となる藻食性魚類の特定を試みたのでそれらの概要を報告する．

なお，報告に先立ち，実験用のブダイを提供していただいた野母崎町水産農林課の秀島明和氏，現地での調査にご協力いただいた野母崎・三和漁業協同組合の職員各位，宇久島でのイスズミの情報を提供していただいた長崎県水産開発協会の桑本淳二氏，本文を校閲して頂いた長崎県総合水産試験場の四井敏雄場長に対し感謝申し上げる．

方　　法

調査を行った長崎県野母崎の小立神岩では，1998年秋にほとんどのクロメにおいて葉状部の欠損現象が発生し（桐山ら, 1999)，クロメ群落の消失が危惧されたが，1999年春までに葉状部が再生して外観上はクロメ群落はほぼ通常の状態に回復した（清本ら，2000). SCUBA 潜水による調査を外見的にはクロメ群落が回復したと思われた1999年3月25日に行った．調査当日午前10時の平均水面下13mにおける水温は17.7℃であった．

地形や海藻の分布状況が調査結果に及ぼす影響を極力避けるために，数種の大型褐藻が比較的均質に混生している平坦な岩盤を調査区域とした (Plate 1a). この岩盤は平均水面下7mにあり，その大きさは約10m×20m，生息するクロメ，ワカメ，ノコギリモク，ウスバノコギリモク，エンドウモクの被度は，それぞれ40, 30, 10, 5, 5%であった．調査区域内から，クロメ成体，クロメ幼体，ワカメ，ノコギリモクをそれぞれ約30本ずつ，ウスバノコギリモクを18本，エンドウモクを17本採取した．

採取した海藻は，西海区水産研究所に持ち帰り，種類ごとに以下の項目について測定・観察し，特徴的な個体について写真撮影を行った．クロメについては，石田・由木（1996）に従って年齢査定を行い，全長，中央葉長，最大側葉長を測定した．また，同一年級群の健全な個体との比較によって，葉状部の量が健全な個体の半分以上か以下かを判定した．ワカメ，ノコギリモク，ウスバノコギリモク，エンドウモクについては全長を測定し，健全な個体との比較によって葉状部の面積が健全な個体の半分以上か以下かを判定した．弧状の採食痕の有無を，クロメ成体においては清本ら (2000) と同様に中央葉と成長点付近に分けて，クロメ幼体では葉状部全体で，ワカメにおいては，側葉（羽状葉)，先端，中肋，茎葉移行部（胞子葉の上から櫛歯状の葉が存在する部分)，胞子葉（成実葉）に分けて調べた．ノコギリモク，ウスバノコギリモク，エンドウモクについては，各個体の主枝について，1個体が複数の主枝を持つ場合は長さが上位3本の主枝を選び，主枝先端の生長点と，葉における弧状の採食痕の有無を調べた．

海藻の種類に対する藻食性魚類の採食選択性を検定するために，観察した個体数と採食痕のある個体数を基に，Steel-Dwass の方法（永田・吉田, 1997）により多重比較を行った．

冬季に調査海域に分布する大型の藻食性魚類としてブダイが想定されたため，1999年3月26日に野母崎町地先水域で刺し網により混獲されたブダイ2個体から上下の顎を採取し，これを人為的にワカメ中肋に押し当てることで歯形を付け，これと採集されたワカメに

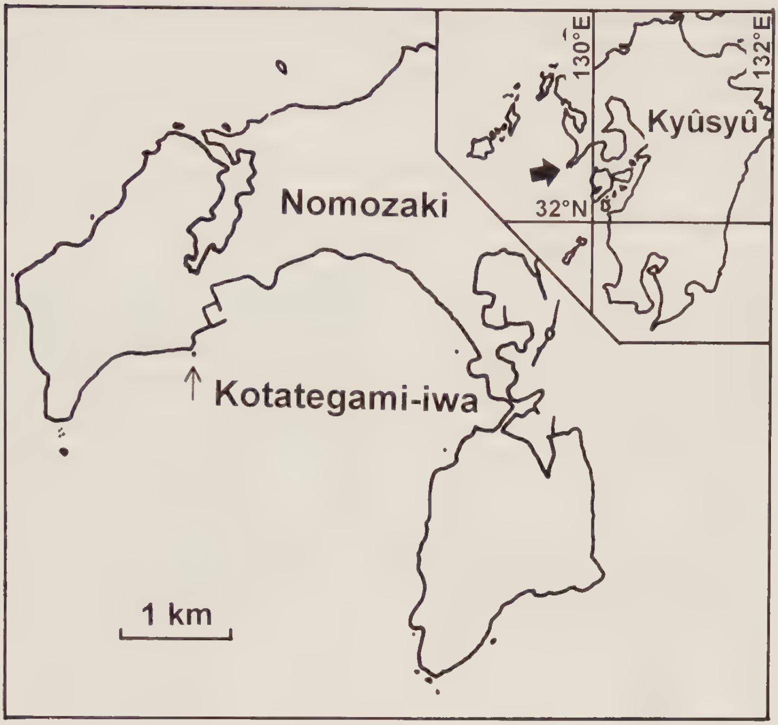


Fig. 1. Map of study site.

見られた弧状の採食痕との比較を行った．

結　　果

採集したクロメの成体は，2歳が主体であったため，2歳のもの31個体について測定を行った．これらの全長は28～51cm（平均41.0cm）で，中央葉長は20～47cm（平均34.7cm），最大側葉長は11～30cm（平均19.5cm）であった（Table 1）．採食痕が中央葉に見られたものは7個体で，生長点付近に見られた個体はなかった．また，側葉面積が半分以下の個体は1個体であった．

クロメ幼体については，側葉が形成されていないもの30個体を測定した．全長は6～33cm（平均22.2cm）であり，採食痕が葉状部に見られたのは2個体で，葉状部の面積が半分以下の個体はなかった（Table 1）．

採集したワカメ30個体（全長21～116cm，平均76.9cm）では多くの個体で葉状部が著しく欠損していた（Plate 1b, c）．側葉が健全な個体の半分以上あったものは4個体のみであり（Table 2），いずれも全長50cm未満の小型個体であった．採食痕は28個体で確認され，部位別には側葉（28個体），先端（21個体），中肋（10個体，Plate 1d），胞子葉（8個体，Plate 1e），茎葉移行部（2個体）の順であった．特に中肋においては弧状の採食痕が葉状部より明瞭で，これらの弧状の両端を結ぶ弦は5～48mm（平均23.9mm）で，特に15～30mmが多く，全体の80％を占めた（Fig. 2）．また，2個体では中肋に弧状の傷が同一部位の両面に見られ，これらの弦はそれぞれ22.0mm，13.7mmであった．

ノコギリモク30個体（全長13～50cm，平均28.6cm）では，観察対象とした主枝73本のうち頂端部が切れて生長点のないものは11本であった（Table 3）．葉に採食痕がみられたものは1個体のみであり，葉の面積が半分以下のものはなかった．

Table 1. The size of *E. kurome* and the proportion of individuals having blade less than half of normal one, and having arc-shape scars on their blade.

Age	Number	Length (mean±SD cm)			Half blade lost*		Arc-shape scar			
		Total (Min.-Max.)	Primary blade (Min.-Max.)	Longest lateral blade (Min.-Max.)			Primary blade		Near growth point**	
					No.	%	No.	%	No.	%
2	31	41.0±5.6 (28-51)	34.7±6.0 (20-47)	19.5±4.7 (11-30)	1	3	7	23	0	0
0	30	22.2±5.6 (6-33)	20.9±4.9 (6-31)		0	0	2	7		

*Number of individuals whose area of lateral blades (2 years old) and blades (0 year old) were less than a half of normal one.
**Five lateral blades from transit part of stipe to blade.

Table 2. The size of *U. pinnatifida* and the proportion of individuals having blade less than half of normal one and having arc-shape scars.

Number	Total length mean±SD cm (Min.-Max.)	Half blade lost*		Arc-shape scar existed									
				Lateral blade		Top		Midrib		Transit part**		Sporophyll	
		No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
30	76.9±20.7 (21-116)	26	87	28	93	21	70	10	33	2	7	8	27

*Number of individuals whose blade area were less than a half of normal one.
**Transit part of stipe to leaf.

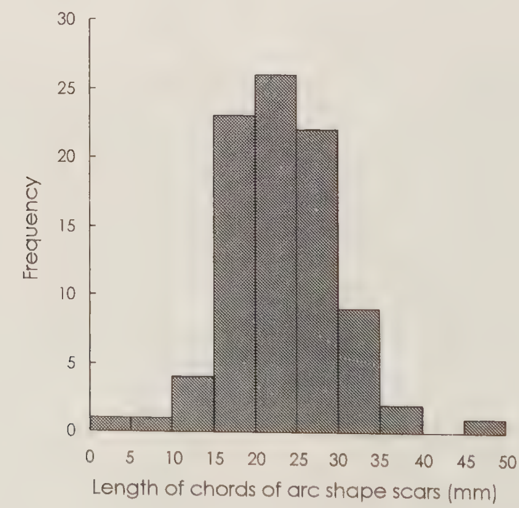


Fig. 2. Size frequency of chords of arc-shape scars on the midrib of *Undaria pinnatifida*.

Table 3. The size of the Sargassaceous algae and the proportion of having arc-shape scars and having blades less than half of normal one and having the main stems without apical growth point.

Species	Individuals	Total length mean±SD (cm) (Min.–Max.)	Arc-shape scars No.	Arc-shape scars %	Half blade lost* No.	Half blade lost* %	Number of main stem	Growth point lost No.	Growth point lost %
S. macrocarpum (ノコギリモク)	36	28.5±8.5 (13–56)	1	3	0	0	73	11	15
S. serratifolium (ウスバノコギリモク)	18	64.7±13.4 (46–93)	0	0	0	0	27	4	15
S. yendoi (エンドウモク)	17	28.9±13.0 (12–59)	0	0	0	0	41	10	24

*Number of individuals whose leaf area were less than a half of normal one.

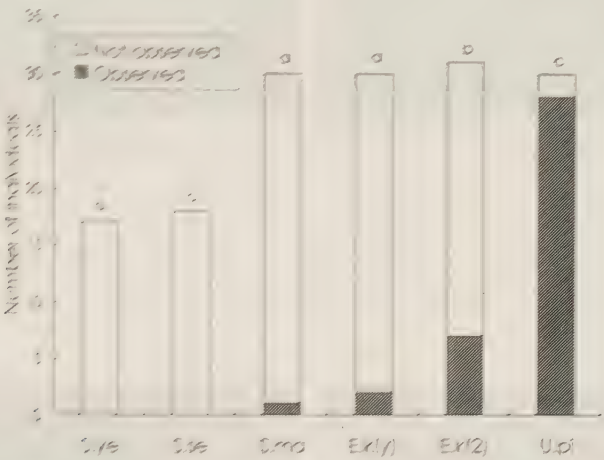


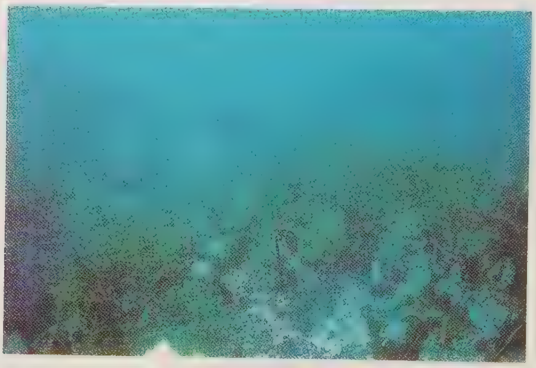
Fig. 3. The occurrence of arc-shape scars on the five brown macroalgae. Observed (shaded), not observed (clear). Alphabet characters above the bars show the result of multicomparison by Steel Dwass method.
S.ma: *Sargassum macrocarpum*, S.ye: *S. yendoi*, S.se: *S. serratifolium*, E.k(y): young *Ecklonia kurome*, E.k(2): 2 years old *E. kurome*, U.pi: *Undaria pinnatifida*.
a vs. b: $p<0.05$, a vs. c and b vs. c: $p<0.001$.

ウスバノコギリモク18個体（全長46～93cm，平均64.7cm）では，主枝27本のうち頂端部が切れて生長点のないものは4本であった（Table 3）。葉に採食痕が見られたものや葉の面積が半分以下のものはなかった。

エンドウモク17個体（全長12～59cm，平均28.9cm）では，主枝41本のうち，頂端部が切れて生長点のないものは10本であった（Table 3）。葉に採食痕が見られたものや葉の面積が半分以下のものはなかった。

以上の各褐藻について，測定した個体のうち，採食

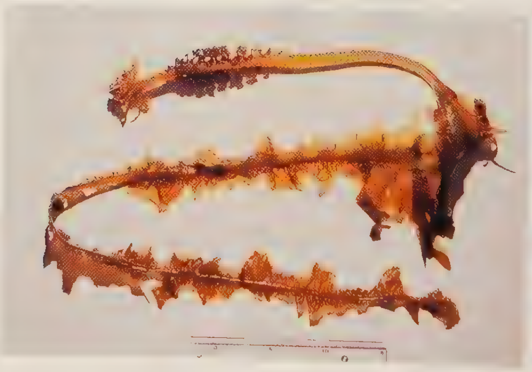
Plate 1. Photographs of sampling site, sampled *Undaria pinnatifida* and the teeth of *Calatonus japonicus*.



(a) Sampling site.



(b) Blade disappearing *U. pinnatifida* at collecting site.



(c) Blade disappearing *U. pinnatifida*.

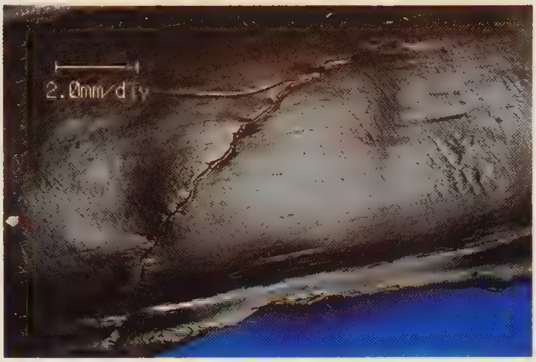


(d) Arc-shape scars on the midrib.

Plate 1. (cont.)



(e) Scars on the sporophyll.



(f) Bite mark found on the midrib.



(g) Artificial bite mark made by pressing the teeth of *C. japonicus*.



(h) The upper teeth of *C. japonicus*. The length between allows were measured as the chord in Table 4.

Table 4. The length of chord and between teeth of *C. japonicus* as shown in Plate 1(h)

	Body length (cm)	Upper teeth		Lower teeth	
		Chord* (mm)	Distance between teeth Min.-Max. (mean) (mm)	Chord** (mm)	Distance between teeth Min.-Max. (mean) (mm)
No. 1	43.4	18.9	0.8-2.0 (1.6)	19.7	0.8-2.1 (1.5)
No. 2	31.8	14.8	0.6-2.2 (1.2)	13.4	0.7-1.6 (1.1)

*The length between allows in plate 1h.
**The length of the part to engage with the measuring part of the upper teeth.

痕の見られた個体数を Fig. 3 に示した．採食痕の見られた割合は各海藻によって異なっており，エンドウモク，ウスバノコギリモク，ノコギリモクではほとんど見られず，クロメは幼体で７％，２歳で23％であったのに対して，ワカメでは93％と他に比べて非常に高い割合であった．Steel-Dwass の方法による多重比較でも，ワカメは他のいずれよりも統計的に有意に（$p<0.001$）高い値であった（Fig. 3）．また，クロメ２歳でもクロメ幼体，エンドウモク，ウスバノコギリモク，およびノコギリモクと比較して有意差（$p<0.05$）が認められた．

ブダイ２個体の上下の顎歯の測定結果を Table 4 に示す．上顎の弦は，口を開いた状態で側面の飛び出た歯の前方基部間の距離とし（Plate 1h），下顎については上下の顎歯を噛み合わせた上で，上顎と対応する場所を計測した．上下の顎の弦は13.4～19.7㎜であり，調査海域から採集されたワカメに見られた弧状の採集痕の弦の範囲（Fig. 2）に該当した．ワカメ２個体の中肋に残された弧状の細かい傷（Plate 1f）では波状型の隣接した凸部間の距離は1.3～1.7㎜（平均1.5㎜，n＝7）であり，２個体のブダイの歯間距離0.6～2.2㎜と近似していた．採集されたワカメの中肋に残された弧状の傷（Plate 1f）と比較すると全体的な形状や断面の細かい波状の痕は，体長31.8㎝のブダイの下顎歯をワカメ中肋に押し当てて得られた歯型（Plate 1g）に酷似していた．

考　　察

今回観察を行った野母崎の潮下帯に生育する大型褐藻５種において，種によって採食痕の見られる頻度が大きく異なった．採食痕がもっとも多かったのはワカメで，観察した93％の個体に，次いで多かったクロメでは年齢で異なり，２歳では23％，幼体では７％であった．一方，ホンダワラ類のエンドウモク，ウスバノコギリモク，ノコギリモクで採食痕が明瞭に認められた個体は３％以下と少なかった．しかし，ホンダワラ類では葉や枝が細く採食痕が判別しにくく，主枝頂端が切れて生長点がないものを採食された個体としても，ノコギリモク15％，ウスバノコギリモク15％，エンドウモク24％に過ぎず，藻食性魚類による採食は起こっているものの，ワカメに比べると少ないと推察された．

このように，藻食性魚類は顕著な採食選択性をワカメに対して示し，採食痕は側葉のみならず，中肋や胞子葉にも及んでいた．この採食痕は弧状の特徴的な形態をしており，ブダイの顎歯を押しつけて人為的につけた歯形に酷似していたことから，ワカメの採食はブダイによるものと推定された．しかし，クロメやホンダワラ類にみられたものは特徴が少なく，採食痕からは魚種を特定できなかった．

本海域で主要な藻食性魚類と想定されるのはブダイとアイゴであり，これらの種についてはヒロメ *Undaria undarioides* の養殖個体を用いた摂餌試験が行われており，アイゴでは水温20℃を下回ると摂餌活性が落ち，17.5℃以下では全く摂餌しなくなるのに対して，ブダイは水温18℃付近でよく摂餌するという（木村，1994）．静岡県南伊豆のカジメ群落では９～10月にはアイゴ，11～12月にはブダイの採食が盛んで，同一カジメ個体が秋から冬にかけて両魚種の採食を相次いで受け，葉状部が消失することが判明している（中

山・新井，1999）．本海域でも，3月の調査時点で水温は17～18℃と低く，冬季にはブダイによる採食が卓越していたと考えられる．しかし，調査地から1km離れたところでアイゴが目撃されていること（清本ら，2000），また，宇久島ではイスズミ *Kyphosys vaigiensis* がワカメを飽食し，養殖ワカメに被害が出たこと* 等から，この海域でもブダイのみでなく，アイゴ，イスズミなど他の藻食性魚類についても注意する必要があろう．

今回の結果から，藻食性魚類には強い採食選択性があることが認められた．このため，藻食性魚類の選択的採食を通じて，海藻群落の構造に変化を及ぼす可能性も考えられ，この視点からの調査も必要であろう．

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平成12年６月　発行

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